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Edited by

CARLETON REA and J. RAMSBOTTOM

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THE PETERSFIELD FORAY.

May 17th to 21st, 1929.

The 1929 Spring Foray took place at Petersfield during the Whitsun week-end, May 17th to May 21st, with headquarters at the Old College Private Hotel. Owing to the extraordinarily dry spring very few fungi were expected, and the list of species is the shortest on record. The weather during the week-end was delightful, and compensated to some extent for the disappointment always experienced when hunting is poor.

On Saturday, May 18th, members took the bus to Rogate and spent the whole day in the district known as Harting Combe, north of Petersfield. This was the only ground which gave promise of fleshy fungi, yet very few species were encountered and none in any quantity. In the evening, at headquarters, Mr Ramsbottom gave an interesting talk on Fermentation, dealing with various organisms concerned and recent work.

Sunday morning was spent in a visit to Bedales School, where the hall, library, and laboratories were inspected, and the science master, Mr F. R. Browning, explained the methods of work in the school. In the afternoon, by kind permission of Mrs Alan Lubbock, woods and pastures at Adhurst were worked through. Among various resupinate Hymenomycetes met with here the most interesting was *Tulasnella microspora*, first described from a collection made by Mr Pearson in Surrey.

In the evening, after a short walk to see the ancient "barrows" on Petersfield Heath, under the guidance of Mrs Harrington, a business meeting was held. Various suggestions were made as to a suitable locality for the Spring Foray in 1930. After some discussion it was decided, on the motion of Mr Gould, seconded by Mr Buddin, that King's Lynn, Norfolk, would be a good centre, provided that the necessary arrangements could be made. As an alternative, Chirk in North Shropshire was voted for. Two new members were elected. At the close of the meeting a very hearty vote of thanks was passed to the landowners who had granted permits for work on their estates, and especially to Mrs Harrington and Mr F. R. Browning, who had assisted so much in the planning of excursions and general arrangements for a very enjoyable week-end.

On Whit Monday the party proceeded by bus to South Harting and arrived just in time to see the opening ceremonies, including a procession of villagers to church, of an old-time Sussex fête. After a visit to the woods near the village the party

split, some members going towards Up Park, while a few decided to keep on lower ground and work back towards Petersfield by way of Goose Green. Neither party found very many fungi, but Mr Hughes discovered a specimen of *Ganoderma lucidum*, and Miss Wakefield one of *Mycoleptodon ochraceum*. Most of the Pyrenomycetes listed were collected by Mr E. W. Mason in the Up Park district.

For assistance in compiling the attached list the Secretary is indebted to all members present, and especially to Mr Mason and Mr Ramsbottom.

The Mycetozoa have been listed by Mr H. J. Howard, and are added at the end of the list of fungi. Owing to the very dry weather, and the fact that the woods visited were largely of beech, the number of species and indeed the number of specimens was very small and hardly worth a separate list.

Complete List of Species gathered during the Foray.

H. = Harting Combe; *A.* = Adhurst; *U.* = South Harting and Up Park; *G.* = Goose Green.

HYMENOMYCETES.

Marasmius conigenus (Pers.) Karst., *H.*
Panus stipticus (Bull.) Fr., *H.*, *G.*
Entoloma rhodopolium Fr., *H.*, *A.*
Pholiota praecox (Pers.) Fr., *H.*, *A.*
Inocybe maritima Fr., *A.*
Galera tenera (Schaeff.) Fr., *H.*
Tubaria furfuracea (Pers.) W. G. Sm., *H.*
Stropharia semiglobata (Batsch) Fr., *H.*
Hypholoma fasciculare (Huds.) Fr., *H.*, *A.*, appendiculatum (Bull.) Fr., *U.*
Psathyrella disseminata (Pers.) Fr., *U.*, atomata Fr., *U.*
Panaeolus campanulatus (Linn.) Fr., *A.*
Lenzites betulina (Linn.) Fr., *H.*
Polyporus betulinus (Bull.) Fr., *H.*, adustus (Willd.) Fr., *A.*, *U.*
Fomes connatus Fr., on apple, *H.*, pomaceus (Pers.) Big. & Guillem., *Petersfield*, ferruginosus (Schrad.) Mass., *H.*, *A.*
Ganoderma lucidum (Leyss.) Karst., *U.*, applanatum (Pers.) Pat., *U.*
Polystictus versicolor (Linn.) Fr., *H.*, *A.*, *U.*
Trametes gibbosa (Pers.) Fr., *H.*, *U.*, rubescens (Alb. & Schwein.) Fr., *H.*
Daedalea quercina (Linn.) Fr., *H.*
Merulius Corium (Pers.) Fr., *H.*
Mycoleptodon ochraceum (Pers.) Pat., *G.*
Odontia farinacea (Pers.) Quél., *H.*
Irpex obliquus (Schrad.) Fr., *A.*, *G.*
Stereum rugosum (Pers.) Fr., *A.*, hirsutum (Willd.) Fr., *H.*, *U.*
Hymenochaete rubiginosa (Dicks.) Lév., *A.*
Corticium laeve (Pers.) Fr., *H.*, comedens (Nees) Fr., *A.*, porosum Berk. & Curt., *A.*, praetermissum (Karst.) Bres., *H.*
Peniophora cremea Bres., *A.*, quercina (Pers.) Cooke, *H.*, *A.*
Solenia anomala (Pers.) Fr., *A.*
Auricularia mesenterica (Dicks.) Fr., *H.*
Exidia Thuretiana (Lév.) Fr., *U.*
Tulasnella incarnata Juel, *H.*, microspora Wakef. & Pears., *A.*

GASTEROMYCETES.

Scleroderma aurantium Pers., *A.*

UREDINALES.

Uromyces Ficariae (Schum.) Lév., *H.*, Scillarum (Grev.) Wint., *A.*
Puccinia Violae (Schum.) DC., *H.*, *U.*, Saniculae Grev., *U.*, variabilis Grev., *H.*, Caricis (Schum.) Rebent., *A.*
Triphragmium Ulmariae (Schum.) Link, *A.*
Phragmidium Sanguisorbae (DC.) Schroet., *U.*, Rubi (Pers.) Wint., *H.*
Milesina Dieteliana (Syd.) P. Magn., *H.*

PYRENOMYCETES.

Hypocrea fungicola Karst. on *Polyporus betulinus*, *H.*
Bertia moriformis (Tode) de Not., on *Hazel*, *U.*
Melanomma pulvis-pyrius (Pers.) Fuck., on *Hazel*, *H.*, *U.*
Mycosphaerella maculaeformis (Pers.) Schroet., on *leaves of Oak and Chestnut*, *H.*
Hypospila Pustula (Pers.) Karst., *U.*
Ditopella fusispora de Not., on *Alder*, *A.*
Diaporthe leiphaemia (Fr.) Sacc., on *Oak*, *H.*, taleola (Fr.) Sacc., on *Oak*, *H.*
Eutypa spinosa (Pers.) Tul., on *Beech*, *U.*, flavovirens (Fr.) Tul., on *Hazel*, *A.*
Cryptosphaeria eunomia (Fr.) Fuck., on *Ash*, *H.*, *U.*
Cryptospora corylina (Tul.) Fuck., on *Hazel*, *H.*
Melanconis stilbostoma (Fr.) Tul. conidial, on *Birch*, *H.*, Alni Tul., conidial, on *Alder*, *A.*
Pseudovalsa lanciformis (Fr.) Ces. & de Not., on *Birch*, *H.*
Calosphaeria pusilla (Wahlenb.) Karst., on *Birch*, *H.*
Quaternaria quaternata (Pers.) Schroet., conidial, on *Beech*, *H.*
Diatrypella verrucaeformis (Ehrh.) Nits., on *Beech*, *H.*, *U.*, favacea (Fr.) Nits., on *Birch*, *H.*
Diatrype Stigma (Hoffm.) de Not., on *Birch*, *H.*, on *Beech*, *H.*, *A.*, *U.*
Hypoxylon semiimmersum Nits., on *Oak*, *H.*, multiforme Fr., on *Birch*, *H.*, *A.*, on *Beech*, *U.*, purpureum Nits., on *Ash*, *U.*, fuscum (Pers.) Fr., on *Hazel*, *H.*, *G.*, on *Alder*, *A.*, argillaceum (Pers.) Berk., on *Ash*, *U.*, coccineum Bull. on *Birch*, *H.*, on *Oak*, *G.*, serpens (Pers.) Fr., on *Oak*, *G.*
Ustulina vulgaris Tul., *H.*, *U.*
Xylaria Hypoxylon (Linn.) Grev., *H.*, carpophila (Pers.) Fr., *H.*, *U.*
Endodothella Junci (Fr.) Theiss. & Syd., *H.*
Rhopographus Pteridis (Sow.) Wint., *H.*, *A.*

DISCOMYCETES.

Morchella Smithiana Cooke, *A.*
Calycella citrina (Hedw.) Quél., *U.*
Bulgaria inquinans (Pers.) Fr., *H.*
Chlorosplenium aeruginosum (Oeder.) de Not., mycelium only, *H.*, *A.*
Helotium fructigenum (Bull.) Fuck., *H.*
Dasyscypha virginea (Batsch) Fuck., *A.*
Hyaloscypha hyalina (Pers.) Boud., *A.*
Micropodia pteridina (Karst.) Boud., *H.*
Urceolella Pteridis (Alb. & Schwein.) Boud., *H.*
Mollisia cinerea (Batsch) Karst., *H.*, *A.*, *U.*
Tapesia fusca (Pers.) Fuck., *A.*
Stegia Ilicis Fr., *H.*

PHYCOMYCETES.

Synchytrium Taraxaci de Bary & Wor., *U.*

DEUTEROMYCETES.

Phyllosticta hedericola Dur. & Mont., *A.*
Septoria Rubi West., *H.*
Catinula turgida (Fr.) Desm., on *Hazel*, *H.*

Ovularia obliqua (Cooke) Oud., *H.*
Rhinotrichum repens Preuss, *A.*
Bispora monilioides Corda, *H.*
Helminthosporium Smithii B. & Br., on *Holly*, *H.*

MYCETOZOA.

Didymium squamulosum Fr., *H.*
Lycogala epidendrum Fr., *H.*, *A.*, *U.*
Reticularia Lycoperdon Bull., immature, *H.*
Comatricha nigra Schroet., *H.*, *U.*
Craterium minutum Fr., probably, orange plasmodium only, *H.*
Trichia persimilis Karst., *H.*, *A.*, *U.*, varia Pers., *A.*
Arcyria incarnata Pers., *A.*

THE BRISTOL FORAY.

September 30th to October 5th, 1929.

The thirty-third Autumn Foray and Annual General Meeting were held at Bristol during the week September 30th to October 5th, and was attended by about thirty-five members, together with some delegates from the Imperial Mycological Conference who joined the excursions in the latter part of the week.

By kind permission of the Vice-Chancellor one of the laboratories and a lecture room in the Botanical Department were set aside for the use of the Society, and Professor Darbishire and his staff provided everything in the way of equipment that members could wish. The facilities for work were ideal, and only the weather proved unpropitious. An intensely dry, hot summer, lasting until the actual week of the foray, had provided the worst possible conditions for the growth of fungi. In fact very little was to be expected, consequently the list produced, so far from being disappointing, was under the circumstances surprising and very cheering. As compared with the usual foray list, however, it is remarkable for some of its omissions and well illustrates the abnormality of the season. For instance, such common species as *Laccaria laccata*, *Amanita muscaria*, *Russula ochroleuca*, *Lactarius quietus* and species of *Cortinarius* do not appear in the records at all. Only four species of *Russula*, five of *Lactarius*, and eight of *Boletus* is most unusual for these genera in the early autumn. Agarics in general were scarce, and the names listed frequently represent only single gatherings or even single specimens. Just as in the previous year, however, some of the finds were unusual, including such rare forms as *Amanita*

echinocephala, *Lepiota sistrata*, *Psathyra noli-tangere*, *Boletus albidus*, and *Hydnangium carotaecolor**.

Among microfungi perhaps the most interesting records are those of *Sphaerostilbe aurantiaca*, secured by Mr E. W. Mason, and *Sporocybe Azaleae*, found by Mr Deighton on rhododendrons at Blaise Castle. The latter was noted in Britain for the first time only about two years ago, and its record in the recent list of plant diseases appears to be the first published.

The first day's hunting proved to be the best. On this day the party was conveyed by char-à-banc first to two woods, Ball Wood and Corporation Wood, where there was a great deal of fallen wood, and some low-lying, rather damp ground. Later on, towards lunch time, a move was made to Brockley Combe, where members worked up the valley and back by Cleeve Combe. This region proved better for fleshy fungi, but not so good for resupinate Basidiomycetes and microfungi in general.

On Wednesday, October 2nd, two parties were formed. Those interested in pathology visited the Research Station at Long Ashton in conjunction with delegates from the Imperial Mycological Conference, while the others explored the grounds of Ashton Court. At Long Ashton most interesting exhibits and talks had been arranged to illustrate the work of the station, chiefly, of course, in connection with fruit. The party was entertained to lunch and tea, and before leaving very cordial votes of thanks were passed to Professor Barker and his staff, on behalf of both the Imperial Conference and the British Mycological Society.

The party visiting Ashton Court found conditions very dry, and few records were made.

Thursday was spent in the woods of Blaise Castle, and Friday in Leigh Woods. Some additional small excursions were made by some members. Thus Mr Pearson visited Chelwood in Somerset and brought back a number of Basidiomycetes, while Dr Alex. Smith collected Rusts at St Vincent's Rocks. These localities have been added to the official excursions in the list following.

During the week evening meetings were held as usual. On Tuesday evening, at the Annual General Meeting, the Officers and Council for 1930 were elected. Whitby in Yorkshire was selected as the locality for the Autumn Foray in 1930, the date to be fixed by the Council in relation to the International Botanical Conference and the British Association.

* Amongst a few specimens brought to the meeting from other counties, one Polypore proved to be of very great interest, namely *Polyporus albosordescens* Romell, gathered by our member Mr J. S. Hughes. This was found subsequently during this season on *Pyrus Malus*, *Fraxinus*, *Fagus* and *Quercus*. Eds.

On Wednesday evening the President, Miss Wakefield, delivered her Presidential Address, entitled "Fungi Exotici: Past Work and Present Problems."

On Thursday evening, in the Museum lecture theatre, Mr Ramsbottom gave a popular open lecture to the Bristol Naturalists' Society, entitled "The Influence of Fungi on Life in General." The lecture was illustrated with lantern slides, many of them coloured, and was much appreciated by a large audience.

At the final meeting on Friday, October 4th, Mr Rea commented on the finds of the week, and afterwards the thanks of the Society were expressed to all who had helped to make the Foray a success, particularly to Professor Darbishire and his helpers, Professor Barker and Mr Marsh of Long Ashton, Miss Roper, and the various landowners who had allowed access to their ground.

For assistance in compiling the list of species found the Secretary has to thank many members, but particularly Mr Ramsbottom, Mr Pearson, Mr Rea, Mr E. W. Mason and Dr Alex. Smith.

Complete List of Species gathered.

C. = Ball Wood and Corporation Wood, Cleeve Combe and Brockley Combe; *A.* = Ashton Court and Research Station, Long Ashton; *B.* = Blaise Castle; *L.* = Leigh Woods; *V.* = St Vincent's Rocks.

HYMENOMYCETES.

Amanita phalloides (Vaill.) Fr., *C.*, strobiliformis (Paul.) Quél., *C.*, echinocephala Vitt., *L.*

Amanitopsis vaginata (Bull.) Roze, *C.*

Lepiota cristata (Alb. & Schwein.) Fr., *C.*, sistrata Fr., *C.*, seminuda (Lasch) Fr., *C.*

Armillaria mellea (Vahl) Fr., *C.*, *A.*, *L.*

Tricholoma rutilans (Schaeff.) Fr., *B.*, saponaceum Fr., *C.*, inamoenum Fr., *C.*, *B.*, melaleucum (Pers.) Fr., *C.*

Russula nigricans (Bull.) Fr., *C.*, foetens (Pers.) Fr., *C.*, consobrina Fr., *C.*, lutea (Huds.) Fr., *C.*

Mycena flavo-alba Fr., *C.*, rugosa Fr., *C.*, galericulata (Scop.) Fr., *A.*, *L.*, polygramma (Bull.) Fr., *C.*, *A.*, *B.*, filopes (Bull.) Fr., *Chelwood*, haematopus (Pers.) Fr., *B.*, sanguinolenta (Alb. & Schwein.) Fr., *C.*, *L.*, galopus (Pers.) Fr., *C.*, rorida Fr., *L.*

Collybia radicata (Relh.) Berk., *C.*, *B.*, *L.*, longipes (Bull.) Berk., *B.*, fusipes (Bull.) Berk., *C.*, maculata (Alb. & Schwein.) Fr., *L.*

Marasmius peronatus (Bolt.) Fr., *C.*, oreades (Bolt.) Fr., *B.*, erythropus (Pers.) Fr., *C.*, hariolorum (DC.) Quél., *C.*, *L.*, dryophilus (Bull.) Karst., *C.*, ramealis (Bull.) Fr., *C.*, *B.*

Androsaceus rotula (Scop.) Pat., *C.*, *A.*, *B.*, *L.*, androsaceus (Linn.) Pat., *C.*

Lactarius scrobiculatus (Scop.) Fr., *C.*, insulsus Fr., *C.*, vellereus Fr., *Chelwood*, uvidus Fr., *C.*, fuliginosus Fr., *C.*

Hygrophorus eburneus (Bull.) Fr., *C.*

Clitocybe odora (Bull.) Fr., *L.*, rivulosa (Pers.) Fr., *B.*, infundibuliformis (Schaeff.) Fr., *C.*, *L.*, flaccida (Sow.) Fr., *C.*

Pleurotus ostreatus (Jacq.) Fr., *A.*, *B.*, applicatus (Batsch) Berk., *Chelwood*.

Nyctalis asterophora Fr., *Chelwood*.

Panus torulosus (Pers.) Fr., *C.*, stipticus (Bull.) Fr., *Chelwood*.

Pluteus cervinus (Schaeff.) Fr., *B.*, *L.*, phlebophorus (Ditm.) Fr., *C.*
Clitopilus prunulus (Scop.) Fr., *C.*
Paxillus involutus (Batsch) Fr., *C.*
Pholiota mutabilis (Schaeff.) Fr., *C.*, *B.*
Inocybe geophylla (Sow.) Fr., var. lilacina Fr., *C.*
Astrosporina duriuscula Rea, *C.*
Hebeloma fastibile Fr., *C.*
Naucoria badipes Fr., *Chelwood.*
Galera tenera (Schaeff.) Fr., *A.*, hypnorum (Schrank) Fr., *C.*
Tubaria furfuracea (Pers.) W. G. Sm., *C.*
Crepidotus mollis (Schaeff.) Fr., *C.*, *L.*, applanatus (Pers.) Fr., *L.*
Psaliota campestris (Linn.) Fr., *C.*
Anellaria separata (Linn.) Karst., *C.*
Hypholoma fasciculare (Huds.) Fr., *C.*, *B.*, *L.*, radicosum Lange, *C.*, velutinum (Pers.) Fr., *C.*, hydrophilum (Bull.) Fr., *A.*
Gomphidius viscidus (Linn.) Fr., *C.*, *A.*
Psathyra gossypina (Bull.) Fr., *C.*, noli-tangere Fr., *C.*
Coprinus comatus (Fl. Dan.) Fr., *B.*, atramentarius (Bull.) Fr., *A.*, micaceus (Bull.) Fr., *C.*, plicatilis (Curt.) Fr., *C.*
Psathyrella disseminata (Pers.) Fr., *C.*, *L.*
Boletus elegans (Schum.) Fr., *C.*, viscidus (Linn.) Fr., *L.*, granulatus (Linn.) Fr., *C.*, bovinus (Linn.) Fr., *C.*, chrysenteron (Bull.) Fr., *C.*, *A.*, albidus (Roques) Quél., *C.*, satanas Lenz., *C.*, scaber (Bull.), Fr., *L.*
Polyporus squamosus (Huds.) Fr., *C.*, *A.*, intybaceus Fr., *C.*, sulphureus (Bull.) Fr., *A.*, giganteus (Pers.) Fr., *C.*, betulinus (Bull.) Fr., *C.*, *L.*, amorphus Fr., *C.*, adustus (Willd.) Fr., *C.*, Wynnei B. & Br., *C.*, caesius (Schrad.) Fr., *C.*, *A.*, *B.*, *L.*, spumeus (Sow.) Fr., *B.*
Fomes ferruginosus (Schrad.) Massee, *L.*, Ribis (Schum.) Fr., *B.*, *L.*, ulmarius (Sow.) Fr., *C.*, *A.*, annosus Fr., *C.*, *B.*, *L.*, connatus Fr., *C.*
Polystictus versicolor (Linn.) Fr., *C.*, *A.*, *B.*, *L.*
Poria obducens (Pers.) Fr., *B.*, viridans Berk. on *Larch*, *L.*, xantha (Fr.) Lind, *C.*, *L.*
Irpex obliquus (Schrad.) Fr., *C.*, *A.*, *B.*
Lenzites betulina (Linn.) Fr., *C.*, on *Oak*, *L.*
Trametes gibbosa (Pers.) Fr., *C.*, mollis (Sommerf.) Fr., *A.*
Merulius tremellosus (Schrad.) Fr., *L.*, rufus (Pers.) Fr., *C.*
Phlebia merismoides Fr., *C.*
Coniophora puteana (Schum.) Karst., *C.*
Fistulina hepatica (Huds.) Fr., *C.*, *A.*, *B.*, *L.*
Radulum orbiculare Fr., *C.*
Acia uda (Fr.) Bourd. & Galz., *C.*, *B.*
Grandinia granulosa (Pers.) Fr., *C.*, *Chelwood.*
Odontia fimbriata (Pers.) Fr., *Chelwood*, bicolor (A. & S.) Bres., *B.*, farinacea (Pers.) Quél., *C.*, Barba-Jovis (With.) Fr., *C.*, papillosa (Fr.) Bres., *B.*, *L.*
Caldesiella crinalis (Fr.) Bourd. & Galz., *C.*
Hypochnus ferrugineus (Pers.) Fr., *C.*, *Chelwood*, fuscus (Pers.) Fr., *Chelwood.*
Hypochnella violacea (Awd.) Schroet., *C.*
Stereum rugosum (Pers.) Fr., *B.*, sanguinolentum (Alb. & Schwein.) Fr., *L.*, hirsutum (Willd.) Fr., *C.*, *A.*, *B.*, *L.*, purpureum (Pers.) Fr., *B.*, *L.*
Hymenochaete rubiginosa (Dicks.) Lév., *A.*, *B.*, corrugata (Fr.) Lév., *B.*
Corticium laeve (Pers.) Quél., *C.*, *L.*, fuciforme (Berk.) Wakef., *L.*, Sambuci (Pers.) Fr., *B.*, *Chelwood*, confine Bourd. & Galz., *C.*, *B.*, echinosporum Ellis, *C.*, polygonium (Pers.) Fr., *L.*, praetermissum (Karst.) Bres., *C.*, *B.*, *L.*, *Chelwood.*
Peniophora candida Lyman, *B.*, glebulosa (Fr.) Bres., *Chelwood*, cremea Bres. var. Allescheri (Bres.) Wakef., *C.*, velutina (DC.) Cooke, *Chelwood*, setigera (Fr.) Bres., *Chelwood*, hydnoides Cooke & Mass., *C.*, *A.*, *B.*, *L.*, *Chelwood*, gigantea (Fr.) Mass., *C.*, incarnata (Pers.) Cooke, *C.*, cinerea (Fr.) Cooke, *C.*, *B.*, *L.*, laevigata (Fr.) Mass., *C.*, *B.*, quercina (Pers.) Cooke, *C.*
Cyphella alboviolascens (Alb. & Schwein.) Karst., *B.*, villosa (Pers.) Karst., *C.*
Solenia anomala (Pers.) Fr., *C.*, *L*

Clavaria cristata (Holmsk.) Fr., *L.*, cinerea (Bull.) Fr., *C.*, stricta (Pers.) Fr., *C.*
Pistillaria puberula Berk., *C.*, *L.*
Auricularia mesenterica (Dicks.) Fr., *A.*, *B.*, auricula-Judae (Linn.) Schroet., *C.*
Tremella lutescens Pers., *L.*, mesenterica (Retz.) Fr., *C.*, *A.*
Exidia nucleata (Schw.) Rea, *C.*, *B.*, *L.*, Thuretiana (Lév.) Fr., *A.*
Sebacina subhyalina Pers., *C.*
Eichleriella spinulosa (B. & C.) Burt, *C.*
Dacryomyces deliquescens (Bull.) Duby, *A.*, *B.*, *L.*
Femsjonia luteoalba Fr., *C.*
Calocera cornea (Batsch) Fr., *C.*, *L.*, stricta Fr., *A.*, viscosa (Pers.) Fr., *L.*

GASTEROMYCETES.

Cynophallus caninus (Huds.) Fr., *C.*
Phallus impudicus (Linn.) Pers., *C.*
Hydnangium carotaecolor B. & Br., *C.*
Lycoperdon giganteum (Batsch) Pers., *C.*, perlatum Pers., *C.*, pyriforme (Schaeff.) Pers., *C.*, *L.*
Geaster fimbriatus Fr., *C.*
Scleroderma aurantium Pers., *A.*
Sphaerobolus stellatus (Tode) Pers., *B.*, *Chelwood.*

UREDINALES.

Uromyces flectens Lagerh., *C.*, Valerianae (Schum.) Fuck., *L.*, Rumicis (Schum.) Wint., *L.*
Puccinia Violae (Schum.) DC., *C.*, Lychnidearum Link, *L.*, pulverulenta Grev., *V.*, Circaeae Pers., *C.*, *B.*, obtegens (Link) Tul., *A.*, *V.*, Cirsii Lasch., *C.*, Hypochoeridis Oud., *C.*, *A.*, Leontodontis Jacky, *L.*, Le Monnierana Maire, *C.*, Taraxaci Plowr., *A.*, *V.*, Veronicae Schroet. on *V. montana*, *B.*, Glechomatis DC., *C.*, *A.*, *B.*, *L.*, Menthae Pers., *C.*, on *Clinopodium*, *V.*, Buxi DC., *C.*, *B.*, Iridis (DC.) Wallr., on *Iris foetidissima*, *C.*, Caricis (Schum.) Rebent., *B.*, Lolii Niels., *A.*, Baryi (B. & Br.) Wint., *L.*, Poarum Niels., *C.*
Phragmidium Sanguisorbae (DC.) Schroet., *V.*, Rubi (Pers.) Wint., *L.*, violaceum (Schultz) Wint., *C.*, carbonarium (Schlecht.) Wint., *L.*
Kuehneola albida (Kuehn.) Magn., *C.*, *B.*, *L.*
Coleosporium Senecionis (Pers.) Fr., *C.*, *B.*, *L.*, Tussilaginis (Pers.) Kleb., *C.*, *L.*
Cronartium ribicola Dietr., *A.*
Pucciniastrum Circaeae (Schum.) Schroet., *C.*, *B.*, *L.*
Milesina Scolopendrii Syd., *B.*
Melampsora Hypericorum (DC.) Schroet., *C.*, Euphorbiae Cast., *B.*, sp. causing Canker on *Willow*, *A.*
Melampsoridium betulinum (Pers.) Kleb., *C.*, *L.*

USTILAGINALES.

Entyloma microsporum (Ung.) Schroet. on *Ranunculus*, *A.*

PYRENOMYCETES.

Sphaerotheca pannosa (Wallr.) Lév., *B.*, Humuli (DC.) Burr., on *Arctium*, *C.*, *L.*, on *Taraxacum*, *V.*
Podosphaera Oxyacanthae (DC.) de Bary, *L.*
Erysiphe cichoracearum DC. on *Vegetable Marrow*, *C.*, on *Heracleum*, *V.*, tortilis (Wallr.) Fr., *C.*, *B.*, *L.*
Microsphaera Grossulariae (Wallr.) Lév., *A.*
Uncinula Aceris (DC.) Sacc., *C.*, *A.*, *B.*, *L.*
Phyllactinia corylea (Pers.) Karst., *C.*
Nectria cinnabarina (Tode) Fr., *C.*, *A.*, *B.*, *L.*, coccinea (Pers.) Fr., *B.*, Peziza (Tode) Fr., *C.*
Hypomyces rosellus (Alb. & Schwein.) Tul., *C.*
Sphaerostilbe aurantiaca Tul. on *Elm*, *A.*
Bertia moriformis (Tode) de Not. on *Elder*, *C.*
Melanomma pulvis-pyrius (Pers.) Fuck., *C.*

Leptospora spermoides (Hoffm.) Fuck. on *Hazel, C.*
Mycosphaerella Fragariae (Tul.) Lind., *L.*
Venturia Rumicis (Desm.) Wint., *C., B., L.*, pirina Aderh., *A.*
Leptosphaeria acuta (Moug. & Nestl.) Karst., *B.*
Diaporthe leiphaemia (Fr.) Sacc. on *Oak, C.*, decedens (Fr.) Fuck. on *Hazel, C.*, Niesslii Sacc. on *Sycamore, C.*, controversa (Desm.) Fuck. on *Ash, C.*
Eutypa flavovirens Tul., on *Hazel, C., L.*
Peroneutypa heteracantha Sacc. on *Elm, A.*, on *Elder, C.*
Anthostoma turgidum (Pers.) Nits. on *Beech, C.*
Melanconis stilbostoma (Fr.) Tul. on *Birch, C., L.*
Pseudovalsa lanciformis (Fr.) Ces. & de Not. on *Birch, C.*
Sillia ferruginea (Pers.) Karst. on *Hazel, C.*
Quaternaria dissepta (Fr.) Tul. on *Elm, C., A.*
Diatrypella verrucaeformis (Ehrh.) Nits. on *Beech, C.*, quercina (Pers.) Nits. on *Oak, C.*
Diatrype Stigma (Hoffm.) de Not. on *Beech, Hazel* and *Hawthorn, C.*, disciformis (Hoffm.) de Not. on *Beech, C.*
Cryptosphaeria eunomia (Fr.) Fuck. on *Ash, C.*
Valsa ambiens (Pers.) Fr. on *Elm, A.*, Fuckelii Nits. on *Hazel, C.*
Hypoxylon semiimmersum Nits. on *Oak, C.*, rubiginosum (Pers.) Fr. on *Ash, C.*, fuscum (Pers.) Fr. on *Hazel, C., B.*, coccineum Bull. on *Sycamore, C., B.*
Daldinia concentrica (Bolt.) Ces. & de Not., *C., B.*
Ustulina vulgaris Tul., *C.*
Xylaria Hypoxylon (Linn.) Grev., *C., A., B.*, polymorpha (Pers.) Grev., *C., B.*, carpophila (Pers.) Fr., *C.*
Phyllachora graminis (Pers.) Fuck., *L.*
Dothidella Ulmi (Duv.) Wint., *C., A., B.*
Rhopographus filicinus (Fr.) Nits., *C., A.*

HYSTERIALES.

Dichaena quercina Fr., *C.*
Gloniopsis curvata Sacc., *C.*

DISCOMYCETES.

Aleuria vesiculosa (Bull.) Boud., *C.*
Peziza aurantia Pers., *C.*
Ciliaria scutellata (Linn.) Quél., *C.*
Exoascus turgidus Sadeb., *L.*
Calycella citrina (Hedw.) Quél., *A., B.*
Coryne sarcoides (Jacq.) Tul., *C., B., L.*
Bulgaria inquinans (Pers.) Fr., *C., A., B.*
Orbilia xanthostigma Fr., *C.*
Phialea firma (Pers.) Gill., *A.*
Chlorosplenium aeruginosum (Oeder) de Not., *C., L.*
Helotium herbarum (Pers.) Fr., *A.*
Dasyscypha virginea (Batsch) Fuck., *A.*
Trichoscypha calycina (Schum.) Boud., *L.*
Arachnopeziza aurelia (Pers.) Fuck., *C.*
Mollisia cinerea (Batsch) Karst., *C., L.*
Pezicula rhabarbarina (Berk.) Tul., *B.*
Encoelia tiliacea (Fr.) Karst., *L.*
Stegia Ilicis Fr., *L.*
Rhytisma acerinum (Pers.) Fr., *C., A., B., L.*

PHYCOMYCETES.

Peronospora parasitica (Pers.) Tul., *C.*

SPHAEROPSIDALES.

Phyllosticta hedericola Dur. & Mont., *C., B.*
Actinonema Rosae (Lib.) Fr., *B.*
Septoria Rubi West., *C., L.*
Dichomera Saubinetii (Mont.) Cooke on *Sycamore, C.*

MELANCONIALES.

Gloeosporium Ribis (Lib.) Mont. & Desm., *A.*
Marssonina Juglandis (Lib.) Magn., *C.*
Melanconium Hederae Preuss, *C.*
Steganosporium piriforme (Hoffm.) Sacc., *C.*

HYPHOMYCETES.

Oidium alphitoides Griff. & Maubl., *C., A., L.*
Monilia fructigena Pers., *A.*
Ovularia obliqua (Cooke) Oud., *B.*
Trichoderma viride (Pers.) Fr., *B., L.*
Botrytis cinerea Pers., *C.*
Sepedonium chrysospermum (Bull.) Fr., *C.*
Trichothecium roseum (Pers.) Link, *B.*
Ramularia calcea (Desm.) Ces., *C., A., L.*, Primulae Thuem., *C.*, sambucina Sacc., *C., B.*, Taraxaci Karst., *A., L.*, Hypochoeridis Magn., *A.*, lactea (Desm.) Sacc., *C.*
Cladosporium epiphyllum Pers., *B.*
Cercospora Mercurialis Pass., *C., A., B.*
Graphium fissum Preuss on *Elm, A.*
Sporocybe Azaleae (Peck) Sacc., *B.*
Ozonium auricomum Link, *B.*

MYCETOZOA GATHERED DURING THE BRISTOL FORAY.

By G. Lister, F.L.S.

NOTWITHSTANDING an exceptionally dry September, thirty-three species of Mycetozoa were collected during the five days of the Foray. Many of the specimens had evidently matured weeks before, and were in a weathered or mouldy condition, but after a few showery days large growths of *Badhamia macrocarpa*, *B. panicea* and *Diderma floriforme* were developing, and probably with a more favourable season the harvest of the fine mixed woods visited would have been far richer. Among the more notable species found were *Lachnobolus congestus* and *Perichaena chrysosperma*, neither of which is common in Britain!

B. = Ball Wood; *C.* = Cleeve Wood; *A.* = Ashton Court; *Bl.* = Blaise Castle; *L.* = Leigh Woods.

Ceratiomyxa fruticulosa (Mueller) Macbride, *C., A.*
Badhamia panicea (Chev.) Rost. *A., Bl.*
B. macrocarpa (Ces.) Rost. *A.*
Physarum nutans Pers. *B., C., A., L.*
P. viride (Bull.) Pers. *C., L.*
P. psittacinum Ditm. *C.*
P. compressum (Alb. & Schwein.) Rost. *A.*
Fuligo septica (Linn.) Gmel. *B., C., A., L.*
Craterium minutum (Leers) Fries. *C.*
C. aureum (Schum.) Rost. *C.*
Diderma floriforme (Bull.) Pers. *A.*

Diachea leucopoda (Bull.) Rost. *L.*
Didymium nigripes (Link) Fries. *C., L.*
Stemonitis fusca Roth *C., A., L.*
S. herbatica Peck *A.*
Comatricha nigra (Pers.) Schroeter. *B., C., A.*
Lamproderma scintillans (Berk. & Br.) Morg. *Bl.*
Cribraria rufa (Roth) Rost. *A.*
C. tenella Schrad. *Bl.*
Lycogala epidendrum (Linn.) Fries. *C.*
Trichia affinis de Bary *B., C., Bl., L.*
T. persimilis Karsten *B., C.*
T. scabra Rost. *Bl.*
T. varia Pers. *B., C.*
T. decipiens (Pers.) Macbr. *C., A.*
T. Botrytis Pers. *A.*
Arcyria cinerea (Bull.) Pers. *C., A., Bl.*
A. denudata (Linn.) Wettst. *B., C., A.*
A. incarnata Pers. *B., C., A., Bl., L.*
A. nutans (Bull.) Grev. *C., A.*
Lachnobolus congestus (Somm.) Lister *Bl.*
Perichaena chrysosperma (Currey) Lister *Bl.*
P. depressa Libert *Bl.*

LICHENS OF THE BRISTOL FORAY.

By R. Paulson, F.L.S., F.R.M.S.

Showers of rain passing over a small area around Bristol, during the late afternoon and evening previous to the Foray, resulted in lichen vegetation rapidly becoming more conspicuous, less fragile, and more easily separated from stone and wood than it was during the latter period of the great drought which preceded the Foray; consequently the lichens listed on this occasion number more than might reasonably have been anticipated.

Foray activities covered land on which are veteran oaks and other trees of great age. Large blocks and slabs of weathered limestone are a feature of the country, each one of which bears its quota of lichens, though it often consists of duplicates.

Dry and somewhat saturated walls of long standing repaid close examination. Characteristic of the former in the vicinity of Blaise Castle are the countless, expansive patches of yellow *Placodium murorum* together with those of bright orange-coloured *P. callopismum* on the sides of walls facing south or south-west. White sheets of *Crocynia* cover rock and wall in the deep shade of ancient walks through the grounds of Blaise Castle.

Wet walls consisting of loose stone slabs with earth between, were met with on the Long Ashton estate, and are made evident as walls by black, long lines formed by the luxuriant development of *Collema granuliferum.*

Dermatocarpon miniatum was met with upon a rock in a certain amount of shade. It is approximately two and a half miles from the centre of the city.

The list numbers sixty-six species and three varieties. It is greatly increased by a number of species being added to it each day by Miss Lorrain Smith.

Chaenotheca melanophaea Zwackh.
Calicium hyperellum Ach.
C. quercinum Pers.
Placynthium nigrum S. F. Gray
Collema pulposum Ach.
C. cheileum Ach.
C. granuliferum Nyl.
Peltigera canina Willd.
Parmelia physodes Ach.
P. caperata Ach.
P. saxatilis Ach.
P. sulcata Tayl.
P. dubia Tayl.
P. fuliginosa Nyl. var laetevirens Nyl.
P. laevigata Ach.
Evernia prunastri Ach.
Ramalina farinacea Ach.
Usnea florida Web. var. hirta Ach.
Xanthoria parietina Th. Fr.
Placodium murorum DC.
P. callopismum Mer.
P. citrinum Anzi
P. pyraceum Anzi
P. rupestre Branth, & Rostr.
Candelariella vitellina Müll.-Arg.
Physcia caesia Nyl.
Lecanora subfusca Ach. var. chlarona Ach.
L. campestris B. de Lesd.
L. coilocarpa Nyl.
L. atra Ach.
L. Hageni Ach.
L. galactina Ach.
L. varia Ach.
L. parella Ach.
L. calcarea Sommerf.
Pertusaria globulifera Nyl.
P. faginea Leight.
P. pertusa Dalla Torre & Sarnth.
P. Wulfenii DC.
Crocynia lanuginosa Hue
Cladonia sylvatica Hoffm.
C. pyxidata Hoffm.
C. fimbriata Fr.
C. coccifera Willd.
C. macilenta Hoffm.
Lecidea flexuosa Nyl.
L. quernea Ach.
L. Metzleri Th. Fr.
L. jurana Schaer.
Bilimbia aromatica Jatta
B. lignaria Massal.
Buellia canescens de Not.
B. myriocarpa Mudd
Opegrapha atra Pers.
O. betulina Sm.
O. varia Pers.
O. vulgata Ach.
Graphis elegans Ach.
Dermatocarpon miniatum Th. Fr.
Verrucaria viridula Ach.
V. macrostoma DC.
V. nigrescens Pers.
V. rupestris Schrad.
V. integra Carroll
V. sphictrina Nyl.
Acrocordia gemmata Koerb.

PRESIDENTIAL ADDRESS.

By E. M. Wakefield, M.A., F.L.S.

FUNGI EXOTICI: PAST WORK AND PRESENT PROBLEMS.

In the pursuit of any form of knowledge, it is good sometimes to pause and take stock; to survey the ground that has been won and to note where further work is required.

That the occasion of a Presidential Address is considered one particularly suited for such a process of stocktaking is evident

from the subjects chosen by some of my predecessors. In 1897 the first President of the British Mycological Society, Mr G. Massee, spoke of "Mycological Progress during the last sixty years." Miss A. Lorrain Smith in 1907 sketched the history of our knowledge of microfungi. Miss Lister, in 1912, told us of "Past Students of the Mycotozoa and their Work"; and Professor Buller in 1914 gave an account of "The Fungus Lore of the Greeks and Romans," the earliest phase of mycological history. Mrs Rea in her Address in 1915 dealt with "The History of Mycological Illustration"; Dr Paul in 1918 with "The Earlier Study of Fungi in Britain." Mr Rea in 1921 supplemented Mr Massee's first address by tracing "Progress in Mycology" since the founding of our Society. Lastly, Dr Butler in 1927 spoke of "The Development of Economic Mycology in the Empire Overseas."

Dr Butler's address was, I think, an outcome of the development that has taken place within our own Society, and an expression of the fact of which we are all very proud, that the British Mycological Society, since its small beginning in 1897, "over a cup of tea," has steadily grown both in membership and in scope, and can now fairly claim to be the Mycological Society of the British Empire.

Our meeting this year follows immediately the second Imperial Mycological Conference, and we have present members from overseas. It has seemed to me that it would perhaps be of interest to try to give an outline of early work on extra-European fungi. My title, "Fungi Exotici," is taken from the series of descriptions of foreign fungi which were started by Mr Massee in 1898 and have appeared in the *Kew Bulletin* at irregular intervals up to the present day.

The field is too wide to cover fully in one short address, and I propose therefore to deal chiefly with the fungi of tropical and subtropical regions, with special reference to our own Dominions, Colonies and Protectorates. Further, as the economic side has been very fully dealt with by Dr Butler, I may limit myself to a consideration of floristic and systematic work in general.

Although fungi were known to the Greeks and Romans, for our purpose we may ignore the very early records. Systematic botany proper begins with the herbalists of the sixteenth century, who described and illustrated the plants they saw around them. At this period the Cryptogams, including fungi, were not understood. The later herbalists, as Gerard and the Bauhins, enumerated various forms, chiefly in order to indicate those they knew to be edible. The fungi were usually included in a section with sponges and corals (so-called "Fungi lapidei") and the general

attitude of the times towards them may be summed up in the words of Hieronymus Bock (1560)—"Mushrooms are neither herbs nor roots, neither flowers nor seeds, but merely the superfluous moisture of the earth and trees, of rotten wood and other rotten things."

Although in very early times traders had reached India, North Africa, and parts of the West African coast, our knowledge of the outside world may really be said to date from the voyages of discovery of the late fifteenth and the sixteenth centuries.

The discovery of new land was not immediately followed by settlement. English colonisation did not begin until the seventeenth century, when civil war and oppression at home caused private citizens to seek new homes elsewhere. Naturally also the early years of colonisation were far too full of excitement and danger for settlers to turn their thoughts to scientific exploration. However, many foreign flowering plants had been introduced into gardens and were well known at the time of Parkinson's *Paradisus in Sole* (1629). These were mostly continental, but there were a few from Asia, North Africa and Virginia. Exotic Cryptogams were quite unknown, and it is not until much later that the first records of foreign fungi appear, when the English colonies had begun to settle down in comparative peace and stability.

The herbalists were concerned with plants chiefly from the point of view of their use in medicine, etc. Towards the end of the seventeenth century a new epoch in systematic botany began with the work of John Ray, who attempted to classify plants in some sort of natural system, according to what he felt were their affinities. Ray developed a wide correspondence with other botanists of the day, including Sir Hans Sloane, who placed at his disposal the whole of the notes he had made on plants observed during his tenure of a post in Jamaica (1687–89). In Ray's *Synopsis Methodica Stirpium Britannicarum*, published in 1690, occurs the first reference to exotic fungi which I have been able to trace. A list is given (p. 250) of Jamaican plants said by Sloane to be common to Britain and Jamaica. Among them are three fungi, one of which is obviously *Auricularia* ("Jew's Ear"), and another the common mushroom. The third may be an *Amanita* but cannot be identified with certainty. In Sloane's *Catalogus Plantarum quae in Insula Jamaica sponte proveniunt*, published in 1696, four fungi are mentioned, and the same four with a few additional notes in his larger work, the *Natural History of Jamaica*, which appeared in 1707. All are referred to British species which had been listed by Ray. Patrick Brown's *Civil and Natural History of Jamaica* (1758) includes

these and various other fungi, arranged according to Ray's system, but with additional generic names based on Micheli's work in 1729.

Ray's most important work was the *Historia Generalis Plantarum*, three folio volumes, of which the first was published in 1686, the second in 1688, and a supplement in 1704. The *Historia* aimed at giving an account as complete as possible of all plants then known. The number of fungi included indicates the advance made in the observation of the lower plants during Ray's lifetime. They are of course for the most part British species but the supplementary volume (1704) contains a list of Virginian fungi, which had been supplied by the Rev. John Banister, a missionary. Some of Banister's fungi were figured by Plukenet in his *Phytographia*, a volume of drawings of rare plants. Among them it is interesting to notice that tab. 116, fig. 7, "Fungus (ex stercore equino), capillaceus, capitulo rorido, nigro punctulo in summitate notato" ("Banister's Virginia Mushroom with dewy heads") is obviously a *Pilobolus*. Among other fungi illustrated are a *Cyathus* (referred by Fries to *C. dasypus* Nees), *Mutinus caninus* (possibly), and what appears to be a species of *Lycoperdon*.

The next writer who mentions tropical fungi is Charles Plumier, a French priest who visited the West Indies three times, in 1689, 1691 and 1696–7. In his folio volume *Traité des Fougères de l'Amérique* (1705) he has two plates with some rather crude figures of fungi. Their inclusion is explained in the preface, where he says that he would have preferred another title than *Traité des Fougères*, because besides ferns he includes other organisms characterised by producing no flower or seed—in fact all plants belonging to Class 16 of Tournefort's "Institutions botaniques."

Of the early works on tropical plants which contain references to fungi, by far the most important is the *Herbarium Amboinense* of Rumphius.

Georg Eberhard Rumpf (Latinised as Rumphius) has been called the "Pliny of the Indies." He was born in 1627, entered the service of the Dutch East India Company, and was sent to Java. In the latter part of 1653 he reached Amboina, a small island lying between Celebes and New Guinea, where he remained for the rest of his life. A keen naturalist, he began the preparation of the *Herbarium Amboinense* soon after his arrival, writing descriptions and making figures of the plants as he found them.

In spite of extraordinary ill fortune, he continued the work almost up to the time of his death. In 1670 he became blind, as a result of a series of collecting expeditions. He was then helped

by his wife, and by a series of assistants supplied by the Dutch East India Company. After his wife and eldest child were killed in an earthquake in 1674, he received less help, and some of it of little value. A culminating misfortune was the destruction of his house, library and manuscripts by fire, in 1687. His original drawings were lost, but with the help of his son and various assistants he set to work to replace them. Thus it happens that the plates as they now exist were never seen by Rumphius, though he took every possible care to ensure that they should be reasonably accurate. This fact may account for some of the difficulties encountered in interpreting his plants.

The completed work consists of six folio volumes, with a supplementary volume, the *Actuarium*. The manuscript of the first six volumes was forwarded to Holland in 1692, but again misfortune dogged the author, for the ship carrying it was destroyed by the French and the manuscript lost. Fortunately a copy had been kept. The six volumes reached Holland finally in 1697. In 1702 Rumphius died, soon after having completed the supplementary volume. The manuscript remained buried in the archives of the Dutch East India Company until 1736, when Professor J. Burman was authorised to prepare it for printing. The date of publication was 1741–50 for the first six volumes, and 1755 for the seventh, that is, half a century after the author's death.

I have given the details of Rumphius's life and work at some length, partly because of the human interest of this story of perseverance in spite of unparalleled misfortune—Goebel has described him as one of the "heroes" of botany—and partly because of the real botanical importance of the work. Many of Rumphius's descriptions and figures are the only "types" of later binomials. Unfortunately, as in the case of many of these earlier works, no specimens were kept.

The fungi described by Rumphius occupy pages 120–131 in volume VI and are accompanied by two plates in black and white. Certain genera are easily recognisable, as for instance *Lentinus* and *Dictyophora*. A list of Rumphius's fungi, with modern names and critical notes, has been given by Elmer D. Merrill.

No less than eight out of seventeen species described have become types of later binomial names. Of these, *Lentinus Sajor-Caju* Fr., *L. Tuber-regium* Fr., and *Ganoderma amboinense* (Lam.) Pat. are well known. Overeem (*Bull. Jard. Bot. Buitenzorg*, ser. III, vol. V, 1923, p. 280) has identified other Rumphian forms, hitherto not placed, as *Daldinia concentrica*, *Lycoperdon Bovista* and *Volvaria volvacea*.

In other works of this period (first half of the eighteenth

century) there are scattered references to exotic fungi. Thus J. Breynius in his *Prodromus Fasciculi Rariorum Plantarum* (1739) mentions "Fungus infundibuliformis, radice tuberosa, Amboinicus, nobis. Fungus rarissimus Amboinensis, Domini ten Rhyne, qui ex India transmisit." There is little doubt that this refers to *Lentinus Tuber-regium*, and it is interesting to note the remark "rarissimus," for though a species which has been so referred to is apparently locally common in tropical Africa, it does appear to be very rare in the East.

In 1753 appeared a further landmark in the history of systematic botany, namely Linnaeus's *Species Plantarum*. In all the previous works we have considered, it must be remembered that what is now called binomial nomenclature did not exist. There were sometimes accidental binomials, but as a rule each plant required a whole descriptive phrase for its mention. Linnaeus's great service to botany was the establishment of a regular binomial system of nomenclature, and his *Species Plantarum* is the starting-point for the nomenclature of Phanerogams to-day. Fungi, however, occupy so small a place in Linnaeus's works that it is obvious that he took little interest in them. In the *Species Plantarum*, ed. 1, 1753, he listed only ten genera of fungi, and the species mentioned were all European. In the whole of the works of Linnaeus only eight species of exotic fungi are mentioned, odd gatherings which happened to come into his hands. These are *Lycoperdon pistillare* (*Mant. Pl.* 1771, p. 313), *L. carcinomale* (*Sp. Pl.* 1781, p. 453), *Agaricus crinitus*. *Boletus favus* and *B. sanguineus* (*Syst. Nat.*, ed. 10, 1759), *Phallus Mokusin* and *Boletus agaricoides* Thunb. (*Syst. Veg.*, ed. 13, 1774) and *Mucor clavatus* (*Sp. Pl.* 1781, p. 453). His two species of *Lycoperdon* are now included in *Podaxis*. *B. favus* was from China and is believed to have been *Hexagonia apiaria* Pers., but the type specimen does not exist, and the only specimen so labelled in the Linnean herbarium is *Hexagonia tenuis* Hook., as pointed out by Klotzsch many years ago. *B. sanguineus* was from Surinam and is the well-known *Polystictus sanguineus*, common throughout the tropics. *Phallus Mokusin*, also from China, is now *Lysurus*. *Boletus agaricoides* was renamed by Fries *Lenzites Thunbergii*. *Mucor clavatus* is now *Corynelia*, the well-known fungus growing on leaves of *Podocarpus* in South Africa.

For some time after the death of Linnaeus systematists were very conservative in the matter of describing new species, and there was a tendency to refer everything to species known to Linnaeus. Thus Loureiro in his *Flora Cochinchinensis* of 1790 referred his plants to Linnean or Rumphian forms. Fortunately, however, he gave descriptions which were drawn from the

actual specimens which he had before him. Hence Willdenow in 1793 was able to point out that his *Phallus impudicus* was obviously not this species—"differt annulo reflexo reticulato" (probably *Dictyophora*)—and that his *Hydnum auriscalpium* was also very doubtful.

About this time (in 1777, 1780–1) Koenig was collecting in Ceylon, but his fungi were not named until very much later, when Berkeley worked through the collections at the British Museum (1842).

Other works of this period which contained references to exotic fungi were Thunberg's *Flora japonica* (1784) and the *Prodromus descriptionum vegetabilium* of O. Swartz (1788). The latter contained descriptions of various West Indian fungi, which were listed again in his better known work *Flora Indiae Occidentalis* (1806). Many of Swartz's species were good and his specific epithets are still in use, as for instance *Agaricus striatus* (*Lenzites*), *Boletus hydnoides* (*Trametes*), *B. supinus* (*Fomes*), etc.

The year 1801 saw the publication of the *Synopsis Methodica Fungorum* of C. H. Persoon. His was the first serious attempt to classify and describe the known fungi of the whole world. Since the publication of Linnaeus's *Species Plantarum* there had been numerous works which included descriptions and also figures of fungi. Some of these were concerned solely with the fungi, others were floras including all groups of plants. Some names of outstanding mycological importance are those of Schaeffer, Batsch, Bolton, Bulliard, Tode, Sowerby, etc., and that enormous work, the *Flora Danica*. Persoon summarised this previous work as well as adding much that was new. In particular we owe to Persoon the names and descriptions of many microfungi, and his *Synopsis* is to-day, under International Rules, the starting-point for the nomenclature of Rusts and Smuts, as well as of the Gasteromycetes.

Persoon arranged his fungi in classes, orders, genera and species, and gave to each group a brief diagnosis of the distinguishing characters. In place of Linnaeus's ten genera he had seventy-one, grouped with considerable feeling for natural affinities. Thus his order No. 5, Hymenothecii, corresponds roughly to Hymenomycetes of the present day, except that some of the larger Discomycetes were included. Puff-balls and Mycetozoa were put in one group, as having their spores developed in a closed fruit body, but allied genera occur together. References to exotic fungi in Persoon's book are, however, so few that he would appear not to have been well acquainted with such literature as already existed. He obviously depended chiefly on Linnaeus, and we find mention of the species

recorded by Linnaeus, with the addition of *Phallus indusiatus*, which had been described from Dutch Guiana by Ventenat in 1798.

We come now to the first half of the nineteenth century, a period characterised by immense activity and by great achievements in botanical science. So much of importance to botany in general and to mycology in particular was taking place at this time that it is difficult to trace clearly any one line of development. One feature of the late eighteenth and early nineteenth centuries which attracts notice is the number of important voyages of scientific exploration which were undertaken. The long struggles between England and France had left a restless spirit, which no doubt, in part at least, accounted for the marked impulse to explore and colonise other lands. From this country there were Cook's voyages between 1769 and 1774, and Flinders to Australia, taking Robert Brown as botanist, in 1801. From France several voyages round the world were undertaken, the results of some of which are of great importance in the history of our knowledge of foreign fungi. One of the earliest of these was that commanded by La Pérouse, which set out in 1785. The ship was lost, but to the expedition sent in search, with Labillardière as physician, we owe the record of *Aseroe rubra*, picked up in Tasmania.

A journey of interest to mycology was that of Palisot de Beauvois to West Africa in 1804–7. His *Flore d'Oware et Benin* contains descriptions and excellent figures of a few of the larger tropical fungi. Of these the best known are *Lenzites Palisoti* (*Daedalea amanitoides* Pal.) and *Hexagonia hirta*.

Adam Afzelius, a Swedish professor, had collected and made drawings of fungi in West Africa before Palisot (about 1792), but his species were not named until Fries published them much later.

Of still more importance mycologically was the voyage round the world of the frigates *Uranie* and *Physicienne*, in the years 1817 to 1820. The expedition, commanded by Louis Freycinet, with Gaudichaud as botanist, visited various Atlantic and Pacific islands, Brazil, the Cape of Good Hope, Australia and the East Indies. About sixty-three fungi were collected, and those which could be preserved were worked out by Persoon. In an introductory note Gaudichaud states that the equatorial regions were rich in fungi, but that these were chiefly of a coriaceous or woody type. Such well-known species as *Lenzites repanda*, *Hexagonia apiaria*, *Trametes corrugata* and *Cladoderris dendritica* were first described from these collections of Gaudichaud. The types still exist at Paris, though some are in poor condition.

The same botanist (Gaudichaud) accompanied the important voyage of the *Bonite* in 1836–7, the fungi collected being worked out by Léveillé, the other cryptogams by Montagne.

Other important collectors of the period who brought back fungi, but can here only be mentioned in passing, were Humboldt and Bonpland (South America), Meyer (Guiana), Junghuhn (Java), Blume (Java), Poeppig (Cuba), F. J. F. Meyen, who went as surgeon on a voyage round the world on the *Princess Louise* (1830), Telfair (Mauritius), Bertero (Chili), Cuming (Philippines), Drège (South Africa), etc.

This enthusiasm for botanical exploration would have had less important results had it not been that it was encouraged and utilised by botanists of the highest ability at home. Sir Joseph Banks, through whom began the connection of Kew with the colonies, was especially interested in the botanical exploration of new colonies, and had himself visited Newfoundland and accompanied Cook in the *Endeavour*. Robert Brown went with Flinders to Australia, and not only collected but studied his collections on the spot, hence bringing back a wealth of new knowledge and material.

Sir William Hooker, the first Director of Kew, with a passionate desire to travel, but frustrated in his own hopes, exercised a far-reaching influence on other workers. He restored and developed Banks's plan for sending out collectors, obtaining official grants for the purpose. Interested especially in cryptogams, he developed an enormous correspondence and received specimens from all parts of the world. The interest taken by Hooker in botanical exploration is shown in the pages of the journal, which under various titles (*Journal of Botany*, *London Journal of Botany*, *Kew Gardens Miscellany*, etc.) he produced at his own expense between the years 1834 and 1857. In addition to floristic papers by various authors, under the heading "Botanical Information," Hooker published extracts from letters or from journals of various travellers with whom he was in touch. The following extract from a letter of Poeppig's (*Hook. Journ.* 1, 1834, p. 381) is worth quoting as showing the difficulties of work in those days: "Amidst savages and millions of mosquitos, widely separated from any civilised being—quite solitary—the only European in an immense province—without shoes and without clothes—often without a monkey to dine upon—unkindly treated by petty authorities, though protected by the far distant government of Lima—once even a kind of prisoner for the space of three months—under all these privations and dangers, thank God, I did not flag." And later, after enumerating the large collections obtained, a very human touch —"Thus you see how much a man may work, provided he has

nothing else to do but to work. Though surrounded by far greater facilities, I do not accomplish half so much here as I used to do in the heart of the primeval forests of the Amazons — whither, however, I should not like to return after all."

The fungi collected by Humboldt and Bonpland in South America were worked out by Hooker himself, to whom we owe such well-known specific names as *Hexagonia tenuis*, *Polystictus pavonius* and *Trametes fibrosa*. Later, however, all the mycological work was handed over to Berkeley, whose connection with Hooker began with his preparation of the section on fungi for Volume v of the *English Flora* of Sir J. E. Smith.

Contemporary with W. J. Hooker were Fries in Sweden, Montagne and Léveillé in France, Schweinitz in America, and Klotzsch at Berlin, with M. J. Berkeley in this country some years younger than the others mentioned. Schweinitz, who wrote only on North American fungi, will not be considered here.

Elias Fries, the "father of mycology," with his careful and accurate descriptions, very soon showed himself to be head and shoulders above any other mycologist of his own or preceding time. Although the days of the theory of evolution were not yet, Fries had an extraordinary feeling for natural affinities and his arrangement of the Hymenomycetes has been generally used even down to the present day. His first paper, "Observationes Mycologicae, Part I," was published in 1815, and after that there appeared a series of works of the highest importance. The *Systema Mycologicum*, three volumes and appendix, published between 1821 and 1832, is, under International Rules, the starting-point for the nomenclature of all groups of fungi except Rusts, Smuts and Gasteromycetes.

It was a complete account and classification of all fungi known at that date, including early foreign records such as those of Rumphius, Swartz, Palisot, etc. The *Epicrisis Systematis Mycologici*, or *Synopsis Hymenomycetum*, published 1836–8, was a volume dealing with Hymenomycetes only, and bringing up to date Volume I of the *Systema*, which was then fifteen years old. It was the forerunner of the *Hymenomycetes Europaci*, but included also exotic species. Meanwhile foreign species continued to come in to workers in Europe, of whom by this time there were several. Fries in 1845 published an account of Natal fungi collected by Wahlberg (1839–41), and in 1837 and 1860 descriptions of fungi collected and drawn by Afzelius in Sierra Leone.

By far the most important of Fries's works on extra-European fungi was his "Novae Symbolae Mycologici," published in the *Nova Acta Soc. Reg. Upsal.* for 1851. This was primarily an

account of fungi brought back by certain Danish collectors, chiefly Liebmann (Mexico), Oersted (Costa Rica and West Indies) and Didrichsen and Kamphovener (Nicobar and various islands of Oceania). It is considerably more than a mere list, for in addition to including previous records, Fries made an effort to correlate existing descriptions, particularly of Polyporaceae, and to this end borrowed from Berkeley types of species which had been described by him. Some of Fries's introductory remarks concerning the variability of species of Polyporaceae, and his doubt as to the value of numerous species which had been proposed from the examination of single specimens, might well have been written at the present day. He evidently realised the importance of the preservation of type specimens and the necessity for their examination by any worker wishing to understand a group. The result of this work was an outline of a classification of Polyporaceae which has been in use, with modifications, up to the present. The genus *Polystictus* is here used for the first time, and *Fomes* and *Poria* appear as series of *Polyporus*. Further the now large genus *Polyporus* is broken up into the sections *Ovini*, *Lenti*, *Petaloides*, etc., as they were retained by Cooke, Saccardo and other later writers.

The work of Persoon, and still more that of Fries, providing a reasonable classification and accessible descriptions of all known species, had given a great impetus to the study of mycology, and among workers of the early nineteenth century are several of the first rank.

Chronologically, Klotzsch requires mention next. He was Curator of the Museum at Berlin, and interested in fungi. About 1831 he visited England, in order to study the collections of Sowerby and Linnaeus. He visited Sir William Hooker (then at Glasgow), and was given access to his collections of fungi. The results were two important papers published in the journal *Linnaea* in 1832 and 1833 in which were described numerous new species of Hymenomycetes. Later (1839) Berkeley republished Klotzsch's descriptions, with additional species and notes, in the *Annals and Magazine of Natural History*. Among collections included in these notes were those of Telfair (Mauritius), Richardson (from Franklin's second journey to the Polar Sea), Drummond (New Orleans), Wight (East Indies), Guilding (St Vincent) and Bertero (Juan Fernandez). Klotzsch was also responsible for the fungi in the account, published in 1843, of a journey round the world made by F. J. F. Meyen—after whom *Polyporus Meyenii* and *Tulostoma Meyenianum* were named.

Another writer of this date was F. Junghuhn, who in 1838 published a preliminary account of the fungi of Java, with coloured illustrations. As in most of the works of this period,

the fungi dealt with were chiefly the larger Basidiomycetes and Ascomycetes, but Junghuhn included also a few microfungi and Mycetozoa, his figures showing that a microscope had been used in their examination. The microscope had been invented many years before, but early instruments, except simple lenses, were very imperfect. Plumier mentioned having used a microscope during his third journey (1696–7), but no doubt this was only a hand lens. The use of the simple dissecting microscope was spreading in the early years of the nineteenth century, and in 1823 Amici improved the compound microscope and employed a camera lucida. Subsequent improvements led to rapid developments in the study of cryptogams, but as was natural, and is still the case, the knowledge of exotic microfungi lagged behind that of European forms.

With the rise of Léveillé, Montagne and Berkeley to mycological fame, papers on exotic fungi appeared with greater frequency as collections poured in to them. Léveillé was a physician in Paris. He appears to have been of a very modest and retiring disposition, and little is known of him beyond the details given by Decaisne and Cordier in their "orations" at his funeral. He published an important treatise on the structure of the hymenium, and first introduced the microscope into the taxonomic study of the higher fungi. The genus *Hymenochaete* we owe to him. He visited Leiden in order to see Persoon's herbarium and studied there also species found in Java by Blume, Junghuhn, etc. In 1844 he published his first important paper on "Champignons exotiques," in which he described exotic fungi at Leiden (chiefly Javan) and also added the descriptions of new species he detected in the Paris Museum and others received from Miquel, Gaudichaud, etc. As already mentioned, Léveillé worked out the fungi collected by Gaudichaud during his third voyage, in *La Bonite*. In 1846 appeared another important contribution by him, on the fungi preserved in the herbarium of the Museum at Paris. Léveillé described as new a large number of species, many of which stand. It was inevitable that he should make some mistakes, and sometimes described the same species twice over. In judging of his work one must remember the meagre knowledge of exotic fungi of the time, and that the importance of exchanging and comparing types had not yet been fully realised.

Montagne became better known and received greater recognition than did Léveillé. He studied medicine and became a surgeon attached to the navy, and thus had opportunities to travel and collect during his voyages, though his early collections were chiefly of phanerogams. After 1830 he devoted himself entirely to cryptogams, and published numerous

memoirs on collections which came to him from Brazil, Guiana, India, Algeria, Cuba and other countries.

In 1865 he collected together all the species which had been already published by him, together with some new ones, in a volume entitled *Sylloge Generum Specierumque Cryptogamorum*. The arrangement adopted was that of Fries, but the volume is important as an epitome of Montagne's own work.

Meanwhile in this country Berkeley was actively producing papers on exotic fungi, Hooker passing on to him all collections which came into his hands. Among his earliest papers were one on a collection of fungi from Tasmania (then called Van Diemen's Land), and one on the fungi collected by Charles Darwin during the voyage of the *Beagle*. In 1844 began in *Hooker's Journal* the series of "Decades" of descriptions of exotic fungi, which continued until 1856. Some of the more important enumerations of fungi for which Berkeley was responsible were those in Hooker's *Flora Antarctica*, *Flora of Tasmania*, and *Flora of New Zealand*, *Cuban Fungi* (in collaboration with M. A. Curtis) and *Ceylon Fungi* collected by Thwaites and Gardner (in collaboration with Broome).

Between Berkeley and Montagne there was an active exchange of correspondence and specimens. Hence it comes about that co-types of many of Montagne's species are in Berkeley's herbarium, now at Kew, and duplicates of Berkeley's types are to be found in the Montagne herbarium at Paris. Berkeley also corresponded with Fries, and through Curtis received fragments of many of Schweinitz's types of North American fungi. In addition to his numerous floristic papers, Berkeley made some valuable contributions towards our knowledge of the morphology and taxonomy of fungi. He showed that the spores of all pileate fungi are borne externally on basidia, not in asci as many authors had thought, and moreover that the same form of "sporophore" as he called it, occurs in *Lycoperdon*, *Mutinus*, etc. Thus he established the definition of the great group Basidiomycetes. Berkeley's drawings of basidia are very accurate, the oblique insertion of spores being well shown. Obviously he possessed a fairly good microscope—he speaks of magnifying six hundred diameters—yet it is curious that in spite of his important discovery he seems later to have made little use of the microscope, leaving the drawing of microscopic details to his friend Broome.

Meanwhile, on the Continent, important advances were being made in the study of fungi. The brothers Tulasne, in a series of papers and finally in their great work *Selecta Fungorum Carpologia*, showed that many so-called "species" (form species of de Bary) were in reality only stages in the life cycle of other

forms, and that they arose in regular succession. Their proof rested not on cultural work, which was then unknown, but on the observed anatomical continuity of the various forms, the origin of the sporophores in question from one and the same mycelium. This phenomenon they called *pleomorphy*.

The work of the Tulasnes is characterised by extreme care and accuracy, and even to-day is essential to students of certain groups.

The means of proof and explanation of Tulasne's pleomorphy was supplied initially through the work of Pasteur. Anton de Bary first suggested the application of pure cultures to the study of fungi, and developed the use of the hanging drop, and to Brefeld we owe the perfection of technical methods. The revolution which took place in the mycological outlook as a result of Pasteur's work is shown by the fact that in his first edition of the *Comparative Morphology and Physiology of Fungi* (1866), de Bary felt it necessary to include a discussion on the "origin" of these organisms (*i.e.* views for and against spontaneous generation). In his second edition, eighteen years later, he omitted this, and stated in explanation, "I set out in all cases from the assumption that these plants are like all other plants the product of germs, each of which is derived from parents of the same species."

De Bary also in his classical work on Smuts (1853) established clearly for the first time the parasitic relationship of fungus and host plant, and to him we owe the elucidation of the heteroecism of Rusts, and of life histories of the Peronosporales, as well as other fungi.

The change in outlook and improved methods in mycology which followed the work of de Bary and Brefeld bring us to the modern period. Works published after this period seem to us more familiar in character, both as to systems of classification and methods of description.

In the latter part of the nineteenth century collections were pouring into Europe from developing colonies. Botanists were attached to various boundary commissions and exploring expeditions, as that of the *Challenger* in 1872–6. The British Association for the Advancement of Science established committees and provided funds for investigation of certain floras; in 1887 was appointed a committee for investigation of the zoology and botany of the West Indies, and in 1888 one for the purpose of exploring the flora of the Bahamas. With the assistance of the grants made Ramage collected fungi in Dominica and St Lucia up to May 1889, and W. R. Elliot in St Vincent and Anguilla in 1892 and 1896. In the Bahamas a few fungi were collected by Baron Eggers.

All this wealth of material had to be worked out by botanists at home, and naturally could best be done by those stationed at or with access to the great herbaria and libraries. Among the more important authors of papers on exotic fungi one thinks of Paul Hennings and P. Sydow in Germany, Paul Hariot and Narcisse Patouillard in France, the Abbé Bresadola in Trento, Saccardo in Italy, Spegazzini in South America, Roland Thaxter in North America and Cooke and Massee in our own country. With the exception of Spegazzini, who worked in South America and acquired a wonderful knowledge of the fungi of this region, and of Thaxter, all these were, as regards exotic fungi, purely herbarium workers.

The year 1882 saw the publication of the first volume of Saccardo's *Sylloge Fungorum omnium hujusque cognitorum*, that invaluable index to all described species which has continued to the present day. Along with the numerous purely floristic papers which were issued, increasing knowledge of the fungi of the world led to attempts to monograph certain genera. In 1887 we have Patouillard on the genus *Laschia*, followed in 1889 by his important enumeration of species of Polyporaceae referred to *Ganoderma* Karst., which had been established originally for *P. lucidus*. Massee also began in 1887 a series of monographs of genera of the Gastromycetes, followed by Thelephoraceae and other groups. These were of the nature of compilations rather than critical research on species, but they were useful as foundations for later work.

Cooke and Massee wrote on the fungus floras of our own colonies. For material they were indebted to such collectors as Colenso in New Zealand; F. von Muller, F. M. Bailey and L. Rodway in Australia; Ridley and Burkill in Malaya; King, Kurz, Burkill and others in India; Jenman, Bartlett, Hart and Rorer in British Guiana and the West Indies; MacOwan and Medley Wood in South Africa; Scott Elliot in Uganda; and others too numerous to mention.

Hennings is noted especially for his descriptions of fungi from the German colonies and from Brazil. P. Sydow, assisted later by his son H. Sydow (the well-known editor of the *Annales Mycologici*), paid special attention to microfungi, and their names are connected particularly with the fungus flora of the Philippines. Thaxter's best known work has been that on the Laboulbeniales, but he has also contributed much to the elucidation of little-known groups, such as the Endogoneae. He himself collected in Trinidad and Chili, and much of his material has been placed at the disposal of workers in special groups. Evidence of Thaxter's keen eye for interesting species is to be found scattered through papers such as those

of Petch on entomogenous fungi and of Burt on Thelephoraceae.

Two other American workers may be mentioned here although, like Thaxter, they overlap into the present century. W. A. Murrill has worked on the Polyporaceae of America and the Philippines and has described many new species. C. G. Lloyd, by means of his widely distributed publications, did much to encourage and popularise the study of the larger tropical fungi. His work was not scientific and was sometimes misleading, yet his notes and photographs have been the only source of help to many wishing to name their species themselves. The need for something better is urgent.

The two most outstanding names of this period are undoubtedly those of Patouillard and the Abbé Bresadola. Both worked more especially on the Basidiomycetes and developed the use of microscopic characters for the identification and classification of these fungi. Yet their work was distinct in character. Patouillard from the first applied himself to improving the Friesian classification of the Hymenomycetes. Various new groupings of Agaricaceae, and new subdivisions of Polyporaceae had already been suggested. In his *Essai Taxonomique* (1900), Patouillard developed a scheme of classification based on hymenial characters. While open to objections, this classification is certainly an advance towards a more truly natural grouping. It has been adopted by later French authors and is the basis of the arrangement used in Mr Rea's *British Basidiomycetae*.

Bresadola created no new system, but will be remembered most for his patient, critical study of the types of older authors. He borrowed extensively from Kew, Paris, Berlin, Leiden and Upsala, and his notes are to be found on the sheets in all these herbaria. The results of his studies are embodied in critical notes of the utmost value attached to species enumerated in his various papers, such as those on Philippine Basidiomycetes, on the Polyporaceae of Java, and on Congo fungi. In three of his latest papers he gave long lists of synonyms which he considered established through his comparisons of types.

Patouillard died in 1926; Bresadola on June 9th of this year. Systematic mycology is the poorer for two men whose knowledge of fungi was both wide and accurate, and who were ever ready to assist those who sought their help. It is for us to carry on the high tradition which they have left.

These men, although working actively until the time of their deaths, really belonged to the generation of the late nineteenth century. But now with regard to workers in our own time. Dr Butler told us, in his address, that the closing years of the

nineteenth century saw the beginnings of the development of Agricultural Departments abroad, and the appointment of mycologists to whole-time posts overseas. This, I think, marks the beginning of a new era, and the work already done is fruitful in suggestions of what may be. I will not waste your time by repeating what Dr Butler has already so ably dealt with—the work of Petch in Ceylon, of Cunningham in New Zealand, and Cleland and Cheel in Australia, of Pole Evans, Miss Doidge and others in South Africa, of Bunting and Dade in the Gold Coast, and his own work in connection with the fungus flora of India. To these I would add references to such work as that of Alfred Möller on Brazilian fungi, and of Holtermann, Raciborski, Penzig, Koorders, and more recently van Overeem on the fungi of Java.

We are still, however, only on the fringe of real knowledge of tropical fungi. There is much to be done yet before we have anything approaching complete lists of even the larger forms. The collections made by Dummer, Maitland, Small, and recently Hansford in Uganda have indicated what a rich fungus flora exists in eastern Tropical Africa. New and interesting species are constantly coming in. Collectors can still do much valuable work, the more so if they bring to the task keen trained powers of observation. The taxonomist has to take into account all the information available, and his task is rendered much easier when collectors supply notes of details which can only be observed when the fungi are gathered. Apart from descriptions of new forms, there is much to learn as to known species. We know almost nothing of the ecology of exotic fungi. It is inevitable that our local lists are still little more than lists, because our knowledge other than names is in most cases so scanty. I know that the mycologist to a small agricultural department has frequently to be a "Jack of all trades" and has little leisure for extensive collecting. Yet he could provide much valuable information if, when he does collect, he would jot down notes as to habitats, colour, host ranges, seasonal occurrence, even the degree of rarity—in fact, any points which to him as a botanist appear to be worth recording. As instances of what I mean I will mention a few problems that come into my mind. One is as to the host range of timber-destroying fungi. I have a note by Mr Deighton that the fungus *Fomes pachyphloeus* occurs in Sierra Leone only on the tree *Parinarium excelsum*. *F. pachyphloeus* is apparently not uncommon in Uganda and East Africa—various gatherings have been received—but unfortunately in no case has information as to host been given. From Angola I have a record on *Ceiba pentandra*, so that it would be interesting to know whether specialisation to host as in Sierra Leone has been observed elsewhere. For many Poly-

poraceae and Hydnaceae we have no host details whatever. It is of course sometimes impossible to determine the tree on which a fungus is living, but wherever possible the host should be stated. By this means we may gradually accumulate information of great value to both pure mycology and to forestry.

Then there are some curious puzzles as to varying forms—whether two collections sent in are states or forms of one species, or really different. There is in Tropical Africa and Madagascar a *Polystictus* which is just like *P. flabelliformis*, except that the hymenium develops in the centre a smoky tinge, whereas that of typical *flabelliformis* is entirely white. A species called *P. carneo-niger*, originally described from Australia, has an entirely blackish grey hymenium. One wonders whether the African form is an intermediate and the two species only forms of one. I should really appreciate it if someone who has opportunity to observe either would tell me if the fungus starts life with a white hymenium, and if so why and how far does it become discoloured greyish. I have not seen the partly greyish form from any other part of the world except Tropical Africa.

A somewhat similar case occurs in the genus *Ganoderma*. There is a species, *G. mastoporum*, which in the fully developed state, at any rate, has a dark, purplish brown pore surface. I have, however, seen one collection which seems to indicate that it starts white and acquires the dark colour at a late stage. One would like to know, for thereby may hang much confusion.

So much for what may be done by those who set out merely to collect. I am convinced, however, that the greatest advance in our knowledge of tropical fungus floras will come from careful critical work on special groups, which can only be undertaken by mycologists working on the spot.

There are some groups which will never be known unless tackled in this way. Among these are the fleshy fungi such as Agaricaceae, Boletaceae and Discomycetes, and microfungi such as Phycomycetes and Hyphomycetes which cannot be preserved for identification as herbarium specimens. Petch has shown how much can be done with the fleshy fungi. In connection with microfungi there is much scope for cultural work and for infection experiments with those which are parasitic. For instance, there are various Cercosporas on grasses—in East Africa apparently common. A few have been described, chiefly from North America, but little is known of tropical forms. One could give them names of course, according to hosts, but of what real value is that, when one considers that the spore size in these fungi is exceedingly variable, and that probably one species, if it is able to grow on several different genera of grasses, would vary according to the nature of the host?

I could go on giving examples of the many points on which we need information, but will add just one to illustrate the difficulty of the worker at home. There is an Agaric which attacks such trees as cacao and coffee and is the cause of the disease known as "Collar-Crack" in the Gold Coast. When this fungus was sent to me from Uganda, I compared it most carefully in all details possible from preserved material, and could find no single point of difference from our own *Armillaria mellea* except that the general size of the sporophores was less. Petch, from his experience of a similar Ceylon form, considers that it is a distinct species, and he is no doubt familiar with the European form. I do not know how one is to settle such a question as this, seeing that in such a case cross-inoculations with pure cultures are scarcely practicable. It does, however, point to the desirability of workers in the tropics having a preliminary sound knowledge of European species and to the need for facilities for the exchange of workers at home and abroad.

Dr Butler has more than once stressed the need for lists of the fungi of all our dominions and colonies. A beginning has been made, but I want to emphasise the fact that for satisfactory results to be obtained there must be collaboration between workers abroad and those at home. The compilation of local lists from existing literature is a useful and necessary first step, but for a fungus flora that is to be of real value to field workers much more is required. First of all collections, and yet more collections. An odd specimen sent in once in a collection conveys little. Even if named, there is no information as to whether it is common or rare, widely distributed or localised in occurrence. Often such an odd specimen is not typical, or does not agree with the type of the species one thinks it may be, and it is not until a number of gatherings have been made that a fair idea of the range of variation can be obtained. To those who wish to have their collections well named, I would say, send ample material, and do not be afraid of sending again and again, especially from new localities.

Then there is the need for critical examination of existing records. It must be remembered that our knowledge of species and their delimitation has increased enormously within the last forty years. Some idea of the increase in numbers may be gained by comparison of the volumes of Saccardo. The first eight volumes contained 31,914 names. With Volume XXIV, which brings us only to 1920 and excludes the Fungi imperfecti described between 1913 and 1920, the number has risen to 76,878. In the early days of collecting many foreign fungi were referred to European species. We know now that many of the higher fungi are not quite so cosmopolitan as they were formerly

supposed to be, and that the temperature factor at least exercises some influence on distribution. Consequently when one sees the name *Polyporus sulphureus* in an old list of fungi from Tropical Africa one has reason to doubt. Sometimes the specimens representing such old records have been lost, but many of them are to be found in one or other of the large herbaria, and before either compiling or rejecting such names the author of any list that attempts to be critical should see the actual specimens. I hold strongly that authors of fungus floras, equally with those of monographs, should wherever possible have seen the specimens which they list, or if they cannot themselves do this, should seek expert opinion on them. By this means we may reach some degree of accuracy, and until we do so it is useless to discuss the geographical distribution of species.

The actual writing up of large floras must necessarily be done in connection with the larger herbaria, where there are facilities for the consultation of specimens and books, and for the elucidation of the many problems, both of taxonomy and nomenclature, which arise in the course of such work. But anyone who has attempted to compile a reliable list of fungi knows how great is the need for more adequate collections and notes. We need more good collections, and we need mycologists who will make special study of the less known groups. The ideal arrangement would be to have in each colony, in addition to a pathologist, a mycologist who could give his whole time to taxonomic and floristic work. Where a Botanical Garden exists this is not impossible. Thus in Malaya there is now a mycologist attached to the Botanic Garden at Singapore. The policy which is being developed there is that the staff shall devote itself chiefly to the systematic study of the flora, leaving pathological problems to the Agricultural Department at Kuala Lumpur.

In Australia, Dr J. B. Cleland and Mr Cheel have undertaken to produce within the next two or three years a handbook of the larger fungi of Australia. It is a big task, but they are endeavouring to get their species as far as possible named by specialists, and to obtain specimens for comparison themselves. Kew has promised to assist with the resupinate Hymenomycetes which outside Europe and North America are very little known.

Where there is no systematic mycologist available, I can only beg of the hard-worked pathologist to bear the matter in mind, to collect and observe all he can, and to send his collections home for determination.

LIFE-HISTORY STUDIES OF THE SPECIES OF PHOMOPSIS OCCURRING ON CONIFERS.* PART I.

By Glen Gardner Hahn.

(With Plates I, II and III and 29 Text-figures.)

An investigation of the life-history of forms of the genus *Phomopsis* occurring on conifers in all their phases has been undertaken in order to determine the identity and relationship of the various species cited in the literature. This research is an important part of a phytopathological problem which has a particular economic bearing ((3) p. 7). The differentiation of *Phomopsis Pseudotsugae* Wilson, the attributed cause of the Phomopsis disease of *Pseudotsuga Douglasii* Carr. (*P. taxifolia* (Poir.) Britt.) and other conifers (62) from similar forms of the same genus occurring on Douglas fir became a very important mycological problem.

The purpose of the present research was to formulate a groundwork for the study of *Phomopsis Pseudotsugae* and all the other known species of *Phomopsis* on conifers, with particular reference to the Douglas fir. On the basis of previous observations, including those contributed by Wilson and by Hahn (19, 62, 63), it was evident that the Douglas fir is a host for several apparently closely allied *Phomopsis* species. The original descriptions of these organisms are in certain instances very inadequate and confusing; furthermore certain species are apparently so variable that there was no sure way of identifying a *Phomopsis* isolated from the Douglas fir with a previously described member of the same genus.

Whether more than one species of *Phomopsis* occurs on the Douglas fir, and, if so, on what basis they could be separated, needed to be definitely settled in order to carry out comprehensive pathological work with *Phomopsis Pseudotsugae*, which was strongly suspected of being a parasite (62). For this reason numerous forms of coniferous *Phomopsis* were obtained from widely separated sources during the period 1926–8 in Great Britain and on the Continent for the purpose of cultural life-history study. This collection was augmented by a group of

* This paper presents part of the data contained in a thesis entitled, "Life-history studies of species of *Phomopsis* occurring on conifers," submitted for the Ph.D. degree, University of Edinburgh, 1928. Subsequent papers ("The life-history of *Diaporthe conorum* (Desm.) Niessl," "Pathogenicity of conifer Phomopses," unpublished MS.) dealing with other data contained in the thesis will be published shortly.

forms previously isolated (18) from Douglas fir and other conifer hosts from various parts of North America.

An attempt was made to include a consideration of all the *Phomopsis* species known to occur on conifers (with one possible exception, *P. Cryptomeriae* Kitajima & Kamei (28), which will be discussed later). At the same time particular attention was paid to the investigation of the perfect stages of these species. The comparative study of forms concerned itself mainly with those morphological and physiological characters which appeared to be constant, and which furthermore seemed to be most important and practicable for a natural differentiation of the numerous *Phomopsis* forms on conifers.

Isolation of forms.

The forms of *Phomopsis* were isolated from different plant parts including the cones. Where the organism was suspected of pathogenicity, isolations were made from spores taken from pycnidia in direct association with a lesion, or, where spores were lacking, from bits of diseased inner bark tissue removed under aseptic conditions. Isolations were made usually either from single spores, or from spore horn (tendril) plantings on plates of very clear corn meal agar containing 2 per cent. cane sugar. At first the spore dilution plate method was followed, isolated spores being picked off under the microscope on bits of the agar medium soon after germination. Pycnidiospores of all the forms tested germinated readily within twenty-four hours at room temperature. Eight or a dozen single spore isolations were made of a given form. These were all compared culturally to detect any aberrance in individual colony growth characteristics or colour production. It was the general experience throughout the culture study that single spore isolations within a given set agreed excellently with each other. When cultures were obtained from spore horns, subcultures were made by transferring bits of the advancing edge of colonies formed from individual spore tendrils distributed over the surface of an agar plate. A few isolations were also made from advancing edges of single colonies in dilution plates.

Culture media.

It is well known that many fungi vary considerably in their macroscopic and microscopic characters under different environmental conditions. The work of Coons (6) and Leonian (30) has shown that the Sphaeropsidales vary greatly in response to their environment. It is now recognised that a great deal of the disagreement in the past between workers has been due to morphological variations under different conditions. As

Archer (1) has pointed out, the very nature of these variations indicates clearly the need of a standard physiological basis by which we may make morphological comparisons between various types of fruiting structures. Upon such a basis alone can a rational taxonomic classification scheme be formulated, whereby fungus species may be recognised by characters appearing under certain definite prescribed conditions. The development of a nutrient medium by Leonian (30) produced a hard agar medium containing a high food concentration of organic and inorganic substances, favourable generally for both pycnidial and perithecial development.

Culture growth studies of *Phomopsis juniperovora* Hahn (17) indicated that this species and closely related forms (18) grew readily and produced pycnidia on sugar-corn meal agar. Wehmeyer ((53) p. 245) and Archer (1) reported, as a result of their extensive culture studies of species amongst the Sphaeropsidales, that hard oatmeal and Leonian's agars gave splendid results, both being media upon which one could be certain of obtaining pycnidia. On the basis of my previous work, and upon that of Wehmeyer and Archer, the present cultural study of coniferous *Phomopsis* forms was confined to the three media cited above. They will accordingly be referred to as sugar-corn meal agar*, Leonian's agar†, oatmeal agar‡. The *Phomopsis* forms were observed to fruit much more readily upon the sugar-corn meal and the oat agar media than upon Leonian's agar.

The best perithecial development was obtained on "natural media," *i.e.* twigs of various conifers and broad-leaved hosts—*Ulmus campestris* L., *Alnus sitchensis* Sarg. and *Acer Pseudoplatanus* L. All twigs for culture purposes were placed in test tubes containing 5 c.c. of water, and sterilised at fifteen pounds pressure for two hours. The use of a more solid substratum was also conducive to the formation of imperfect fruiting bodies which tended to be more like those produced in nature.

Maintenance of normal cultures.

It was found that certain of the *Phomopsis* forms could be maintained in a condition of normal growth by continued subculturing on hard oat agar; other strains, however, gradually became sterile and one species (*P. conorum*) degenerated soon

* Essentially that given by Harshberger (Text Book Myc. and Plant Path. 1918, p. 608); 2 per cent. agar was used. After the final filtering 2 per cent. cane sugar was added and stirred until completely dissolved; autoclaved for fifteen minutes at fifteen pounds pressure. This medium usually titrated + 3·5, but a little variation did not seem to affect growth.

† That given by Leonian (Am. Journ. Bot. xi (1924), 20–21).

‡ That given by Pethybridge and Murphy (Sci. Proc. Dub. Soc. xiii (1913), 580).

after isolation. A culture was considered normal in which there were abundant fusoid spores typical in size and shape and in which the growth characteristics of the fungus when freshly isolated reappeared in subcultures. To ensure vigorous cultures it was necessary to subculture frequently. Certain forms if grown continuously on the sugar nutrient agar, or on media in which there was an excess of water, appeared to undergo a form of degeneration, and a shortened duration of the vitality of the cultures resulted. Such cultures which had "run out" became sterile and lost their growth characteristics, producing colour reactions quite unlike those obtained when the organism was freshly isolated. It was frequently observed that in cultures which had departed from the "norm" (a term used by Wollenweber, Sherbakoff and others (67), for cultural development, with an optimum degree of all the phases of fungus growth), the mycelium produced a gelatinous type of growth; sometimes the hyphae became immersed and sterile. Non-vigorous cultures could sometimes be revived by transfers to oat agar, but certain forms failed to respond to such treatment. The maintenance of stock cultures on natural (twig) substrata has not been tested. There would appear to be possibilities in this method.

Methods of study and presentation.

In comparative cultures of a group of forms to test the constancy and variability of the physiological characters, the strains were transferred at the same time to the medium upon which their reactions were to be studied, and the entire set of cultures were kept under identical environmental conditions. Duplicate, triplicate, and even more tests were made to make sure that the growth characteristics reported were typical and constant. The inocula used in making subcultures consisted of vigorous bits of submerged as well as aerial mycelium, involving if possible a certain number of fruiting bodies. It was frequently found that where the inocula contained spores the subcultures showed a greater tendency to produce spores in turn than subcultures which were obtained from non-spore-bearing mycelium.

In the macroscopical examination of the culture special attention was given to the amount and the character of growth of the mycelium in the aerial stratum; to the colour of the aerial and submerged hyphal strata; to the occurrence of crystals in or on the medium, formed as a result of the growth of the particular fungus on the medium; and to the types of stromatic fructifications appearing just beneath or on the surface of the middle stratum.

In the microscopical study, the different types of conidia (*A*, *B* and intermediate spores) and conidiophores received special

attention. The observations were recorded by means of camera lucida drawings, and by necessary measurements. Drawings of spores were made of either dead, or living freshly exuded, material mounted in a glycerine mounting medium containing potassium acetate*. Every type of conidium occurring was illustrated but the typical and exceptional ones were designated separately. The microscopical character of the mycelium was found useless for the specific differentiation of forms, therefore no attention was given to it. Pycnidiospore measurements were made, whenever possible, of mature spores which had been exuded from the pycnidium in a spore tendril or droplet. Care was taken not to measure spores in the same field twice. At the outset, a number of fields were examined to estimate the prevailing size and shape of each spore type to be measured. When the particular type showed little variability in shape and size only ten conidia of each were measured; when the material showed considerable variability, at least twenty spores were measured.

In differentiating forms where biometric comparisons were utilised, not less than one hundred measurements of a given spore type were made. Biometrical comparisons were recorded according to the method quoted by Rosenbaum ((39) p. 268) from Reitz and Smith. Such comparisons were based on the relation of the difference of the means to the probable error of the difference between these means, and indicated any significant difference which might exist between spore populations of the forms being studied.

The genus *Phomopsis* Sacc.

The genus *Phomopsis* Sacc. has received considerable attention from pathologists and mycologists on account of the comparatively large number of pathogenes which the genus includes and on account of the fact that many of its species produce the two types of spores, *A* and *B*. The genus appears now to be fairly well founded, particularly when one considers the cultural connections obtained by Wehmeyer ((53), (54), (55), (56), (57), (58), (59)), who has demonstrated repeatedly that the imperfect stages of the species of the *Diaporthe* group are strikingly constant, being usually species of *Phomopsis*.

As originally erected, *Phomopsis* was merely a division of the very large genus *Phoma*, designated in 1884 by Saccardo ((42) III, p. 66) to contain those species with "perithecio subastomo depresso, basidiis demum uncinatis instructae (*Phomopsis*) spermogonia *Diaporthe* sistentes." In 1905 this characteristic

* Mounting fluid plus erythrosin to colour: one part 2 per cent. potassium acetate solution; one part 40 per cent. glycerine in ethyl alcohol; copper acetate to colour just slightly; add erythrosin until a rich colour is obtained.

section was definitely split off by the same author (43) and described as a new genus. At this time as Grove (14) pointed out the real basis of the subdivision was imperfectly understood.

Von Höhnel (24) previously had erected a genus amongst the Melanconiaceae—*Myxolibertella*: "Est *Libertella* vel *Myxosporium* cum sporulis filiformibus et oblongis (vel fusoideis) commixtis." Two years later Bubák (4) stated that he regarded *Phomopsis Lactucae* (Sacc.) Bub. as having both fusoid spores and "*Septoria*-artige Konidien" which were bent at the extremity "hakenförmig" and borne on short somewhat stout cone-shaped sporophores. Saccardo (43) commented on Bubák's conception of the filiform spores occurring in the genus *Phomopsis*, but he himself was not clear concerning the origin and function of these "basidia filiformia."

Von Höhnel in 1906 placed his new genus *Myxolibertella* as a synonym of *Phomopsis*. He was strongly opposed to Saccardo's view of the filiform structures of *Phomopsis* as separated basidia. He regarded them instead as very definite "stylospores," and pointed out that these had been previously rightly designated by the Tulasnes, Nitschke and Fuckel as such. With regard to the fruit body of *Phomopsis*, von Höhnel regarded it only as a cavity in a young stroma which arose before the development of the perithecia, and possessed no walls of its own. He suggested that this type of fruit structure could only belong to the Melanconiales. He did not, however, continue in this opinion, for in his key of the Fungi imperfecti he did not place *Phomopsis* among the Melanconiales ((27) p. 330). He described the genus as forming stromata "mit einem Lokulus" with "Conidien meist spindelig" which were "oft mit hakig gebogenen, fädigen Conidien gemischt."

The same year Traverso (52) in Italy recognised all such forms having fusoid and filamentous-shaped spores as *Phomopsis*, and described these as the imperfect stage of *Diaporthe*. Traverso considered the filamentous bodies as released sporophores.

In 1911 Diedicke further defined the position of the genus by amplifying the well-marked morphological characters of the group. With regard to the "basidia filiformia" he considered them to be truly spores, which he designated as "*B* spores," arising from definite, characteristically shaped sporophores. Diedicke observed the *B* spores to be quite different in shape from the sporophores of the "*A* spores," occurring sometimes alone, and not intermixed with the *A* spores. He seemed to be quite clear with regard to the morphology of the fruit body of *Phomopsis*. He recognised a certain range of variability in the stromatic structure amongst the species of the genus, describing the fruit body as being stromatic, enclosed, erumpent, unilo-

cular, or incompletely divided by the arching of the base and pushing in of the sides so that the body had a chambered appearance.

In 1915 Diedicke continued in his morphological idea of the genus *Phomopsis* as possessing both *A* and *B* spores and the cavity as a "Hohlraum...durch seitliche oder bodenständige Hervorragungen des Gewebes öfter etwas in Kammern geteilt." Curiously enough he wavered in his opinion concerning the *B* spores of the species *Phomopsis Arctii* (Lasch) Trav., for in this particular case he regarded them as "nur abnorme Bildungen."

Grove in 1917 in his monographic treatment of the British species of *Phomopsis* showed no hesitancy in calling the "basidiis uncinatis" of Saccardo by the terms of *A* and *B* spores as previously designated by Diedicke. Grove gave his views on what he considered to be the real difference existing between *Phomopsis* and *Phoma*. Two characters were regarded by Grove ((14) p. 52) as distinctive for the genus *Phomopsis*, (1) the permanent sporophores, and (2) the nature of the pycnidium, which he regarded as bearing little resemblance to that of a typical *Phoma*.

Along with Grove, other investigators generally have considered these much-debated abstricted spore forms as true spores, but a few have been inclined to use the term "free paraphyses" as can be noted in the papers by Reddick(35), by Fawcett(12) and by Cayley(5). The so-called *B* spores which apparently may be regarded as non-functional bodies have resisted all the ordinary methods usually employed to induce germination.

Grove stated that proofs by culture that the form genus *Phomopsis* was the pycnidial stage of *Diaporthe* seemed to be altogether non-existent. By 1923–5, Wehmeyer ((53), (54), (56) pp. 577, 615) was able to cite a considerable number of instances where cultural connections had been obtained between the two. The further extensive researches of this worker together with those of Harter and Field(21, 22), Jenkins(29), Cayley(5), Wolf(66), have collectively contributed further evidence that *Diaporthe* is to be generally considered the perfect stage of *Phomopsis*.

It has come about as a consequence of the cultural life-history studies of species of the genus *Phomopsis* and closely allied genera that we have been able to obtain a truer morphological picture of that genus. In 1926, Wehmeyer ((56) p. 615), who has specialised more than any other investigator on both the morphology and physiology of the Diaporthaceae and their imperfect stages, wrote concerning *Phomopsis*: "The imperfect fruit body consists of a spherical, flattened, or somewhat irregular cavity, which is formed within a more or less well-

developed ectostroma. This ectostroma may occur isolated, or in connection with a perithecial entostroma beneath. There are two types of spores formed, either in separate pycnidia, or usually in the same pycnidium. One type of conidium is long-cylindrical, hyaline, one-celled and usually curved or hamate; the other type is one-celled, hyaline, elliptical to fusoid, and contains two oil droplets." In the description of the pycnidial stage of *Diaporthe oncostoma* (Duby) Fuck., Wehmeyer ((53) p. 248) had previously described the stromatic pycnidial fruiting body of this fungus: "In the simplest and smallest stromata the cavities are irregularly lens-shaped. In the more extensive stromatic formations often formed as the smaller ones, the cavities are larger and frequently form projections from the base or sides of their walls, making an irregular cavity buried in a well-developed stroma. The stromata, furthermore, often become compounded and form large tuberculate masses 2–5 mm. in diameter." In the life-history study of *Diaporthe* sp. ((57) p. 388) he reported the pycnidial locules as being flattened, lenticular, spherical, or irregular in shape.

As a result of a wide study of the cultural life-histories of *Diaporthe*, Wehmeyer ((58) p. 168) concluded the year following "that the size, shape and structure of the pycnidial stroma, pycnidial locule and so-called pycnidial wall are by no means constant, and are very unreliable as diagnostic characters, at least in *Phomopsis* and related form genera."

Other contributions to our present knowledge of the morphology of the genus *Phomopsis* have been made recently by Archer (1), who gave a critical study of the stroma and cavity formation in *Phomopsis Arctii* and in *P. coneglanensis* Trav. He pointed out that two factors, food materials and moisture, were conducive to the production of not only more stromatic primordia per unit area, but also to larger primordia. Where a large, solid mass of stromatic tissue was formed, this was produced by the fusion of many contiguous primordia which had a common enveloping brown layer. In this stromatic mass cavities arose at various points, and if moisture conditions remained favourable these enlarged to become finally confluent, and merged into a single, large irregular cavity. On the other hand, if the substratum suddenly dried out, this development ceased, the cavities remaining separate, and a multilocular fruit body resulted.

An examination of the figures of fruiting bodies given by Diedicke (8) shows these bodies usually with a single chamber. However, in others the chambers are exceedingly irregular, with protrusions from the side walls and floor of the fruiting body which may be regarded as partial septa. The same general types

of fruiting bodies have been figured by Harter and Field (21), Enlows (11), Hahn (17), Cayley (5), Wehmeyer (54, 57, 58, 59) and others.

On the other hand, Roberts (37, 38) has described the fruit body of *Phomopsis Mali* Roberts as plurilocular. Jenkins (29) has also described the imperfect (*Phomopsis*) stage of *Diaporthe umbrina* Jenkins as being either simple (unilocular), or chambered as the result of protrusions developing from the wall. Sydow (51), in the description of *Phomopsis Strobi* Syd. reported the fruit body as being separated up into numerous fully formed or incomplete chambers of various shape and size. Wehmeyer ((55) p. 244) found pycnidia associated with *Diaporthe galericulata* (Tul.) Sacc. in nature, which had a structure composed of more or less blackened stromatic tissue containing one or more locules. *B* type spores were formed in these locules. Wehmeyer stated: "The occurrence of such spores suggests the imperfect stage may be a *Phomopsis*, and these the Beta type of spore, which has not previously been noted."

The tendency for pycnidia to become plurilocular amongst certain of the species of the genus *Phomopsis* corroborates the opinion expressed by Wehmeyer concerning the variability of the pycnidial fruit body. Saccardo's original description of the genus emended by both Diedicke (8, 9) and von Höhnel (27) to include forms not only forming pycnidia with simple unilocular cavities but also fruit bodies with irregular cavities, thereby expressing a tendency to become plurilocular, would appear to need further modification; for forms with simple chambered pycnidia are not outside the pale of our present conception of the genus *Phomopsis*.

On the other hand, the idea of the genus as possessing the two types of spores, *A* and *B*, so recently expressed by Wehmeyer (56) also needs modification. Undoubtedly *A* and *B* spores generally do occur together but certain species which have been carefully investigated are not known to produce them. Among the large number of *Phomopsis* forms studied by Wehmeyer ((58) p. 173; (59) p. 226) that investigator mentioned only two species producing the *A* type spore without the *B*. Where the *B* form does not occur, there is a tendency to regard this type as being merely repressed, but potentially capable of being formed under conditions favourable for the production of *B* spores. Jenkins (29) cited only the *A* type of spore as being produced by the imperfect stage of *Diaporthe umbrina*. Sydow (51) reported the same to be true for *P. Strobi*. Wilson (61) described *P. Pseudotsugae* with both *A* and *B* spores, but later (62) decided that only the *A* type occurred. While, generally speaking, *Phomopsis* has been considered a genus in which both *A* and *B* type

spores are produced, this does not appear to be necessarily always so.

Moreover, the conception of the shape and size of the fusoid spores of the genus also appears to need modification. Saccardo described these as "fusoideo-oblongae rarius ellipsoidae," whereas Diedicke, von Höhnel and Wehmeyer regarded them as spindle-shaped or elliptical to fusoid. Forms of the genus produce not only these shapes described but also spores which are distinctly ovate or oblong with obtuse extremities. The spores may be exceedingly short or comparatively of considerable length.

The presence or absence of *B* spores also applies to species of the genus *Fusicoccum* Cda., an imperfect group which the genus *Phomopsis* closely approaches when forms producing multilocular pycnidia are considered. Such a consideration impresses upon the investigator of forms within the Sphaeropsidales the artificiality of the taxonomic boundaries of genera among the Fungi imperfecti. He realises, moreover, how minute structural differences have been emphasised arbitrarily, without a proper appreciation of the variation of such structures within a given genus. One can hardly agree with Grove (14) who, in separating the genera *Phomopsis* and *Fusicoccum*, decided that when the protrusions from the stromatic walls of the fruit body became more decided, the genus *Phomopsis* became *Fusicoccum*, which he regarded as having typically larger spores. As the present paper shows, this is not so: *Fusicoccum* is the imperfect stage of such genera as *Cryptospora* and *Cryptosporella* ((45), (8) p. 12; (46)) possessing a multilocular stroma entirely ectostromatic, and tending to have in nature the cavities near the surface, or in the lateral portions of the fruiting body. Although certain of the species produce both *A* and *B* type spores, the latter does not appear to be so generally present as in the genus *Phomopsis*. Where *Phomopsis* leaves off and *Fusicoccum* begins can only be determined at best arbitrarily. A reasonable basis for distinguishing these genera can be obtained by a study of correlated characters in a large number of species belonging to the group in which the genus lies. This implies a knowledge of the relationships and variations within the group studied.

Coniferous *Phomopsis*—variability.

Comparatively little systematic investigation has been done on the ecology of the Sphaeropsidales and the data which exist apply only to a limited number of species. So far as *Phomopsis* is concerned, it seems to be the general opinion that the pycnidial stromata vary considerably in size and shape under conditions of artificial culture. One has only to peruse the pathological litera-

ture dealing with *Phomopsis* parasites of agricultural and ornamental host plants to become aware of the comparatively large number of investigators who have described and figured various types of stromatic structures, which they have obtained under different environmental conditions. Polymorphic columnar stromatic masses have been figured and described by Cayley ((5) p. 263), and by Wehmeyer ((55) p. 245). These elongated-cylindrical, irregularly shaped plectenchymatic bodies which were reported by the latter worker for *Diaporthe obscura* (Pk.) Sacc. contained conidial locules which developed at various points. The walls of these locules were composed of thick-walled pseudoparenchymatous dark brown tissue. On the other hand, pycnidia formed in culture may be thin-walled and membranous such as those described by Jenkins ((29) p. 597) for *D. umbrina*, or partially or totally embedded pycnidia, in which the wall, when the spore cavity reaches maturity, may be entirely dissolved, leaving only an opening into the agar, as in the artificially produced pycnidia of *P. Arctii* described by Archer ((1) p. 19).

The conifer *Phomopsis* species grown on the artificial substrata employed in this research have shown great variability in stromatic structure. All of the forms produced compound, tuberculate, multilocular structures varying in size, particularly on oat and sugar-corn meal agars containing plenty of moisture. Polymorphism in certain instances on hard agars and on natural media was most striking. On natural twig media the pycnidial bodies tended to form more as they did in nature, but polymorphic bodies also appeared. *P. occulta* Trav. produced on elm stems elongate, exceedingly slender, flexuous structures (some 5 mm. long), which so closely resembled the perithecial beaks of the perfect stage of this fungus *Diaporthe conorum* (Desm.) Niessl, that at first they were mistaken for them. In these slender stalks of twisted plectenchymatic tissue conidial locules were discovered. In test tubes where moisture conditions were less favourable for excessive vegetative growth, flask-shaped semi-erumpent or superficial simple pycnidia formed, frequently provided with ostioles. With regard to the formation of normal pycnidia, much would appear to depend upon the proper balance of moisture within and without the substratum.

The size of spores produced in culture compared very favourably with those found in nature. Variation occurred, but within a specific range which could be determined by the measurement of a sufficient number of naturally produced spores from several forms of the organism throughout the host range of the species. Spore shape also appeared to be a constant character. Similarity of shape and size between *Phomopsis* spores produced in nature

and in culture has been already reported by Harter and Field (21) for the imperfect stage of *Diaporthe batatatis* Harter and Field, and by Winston, Bowman and Bach (65) for *Phomopsis Citri* Fawcett. Cayley (5), on the other hand, stated that *A* spores procured from mono-ascospore cultures of *D. perniciosa* Marchal on hard agars were rather undersized (shorter and wider) than typical pycnospores found in nature. She did not state if this reduced size was still within the actual spore range of the fungus.

In forms producing both *A* and *B* type spores there was a certain amount of variability in the relative production of these different types. Some forms produced both types readily, others were found to produce only one type or the other, under the same set of environmental conditions, *e.g.* a form of *Phomopsis occulta*, No. 43965, isolated from the inner bark of a dead terminal of *Abies pectinata* DC. (collected in the Jura, France), produced only *B* spores.

The conidiophores varied from very short and abbreviated processes to longer, subulate, flexuous structures, but they also appeared to have a fairly definite specific range and to be constant in shape.

Culture growth characteristics were particularly constant for the forms studied, provided the cultures were normal. *Phomopsis Pseudotsugae*, cultured continuously for six years, and *P. juniperovora*, for a slightly shorter period, did not lose their ability to reproduce their characteristic colours under artificial conditions despite the fact that the cultures were kept in diffuse light. The latter fungus produced the flaming orange crystals repeatedly with each subculturing during this extended period. Crystals likewise formed on the surface of sterile twigs in culture. The colour of the extruded spore tendrils, however, showed great variation, varying from whitish to yellowish, becoming sometimes pinkish or orange. There was a general tendency for the spore horns to become whitish or yellowish.

Morphological characters and their taxonomic use.

In classifying the numerous forms of *Phomopsis* isolated from conifers, particular attention was paid to those morphological characters which indicated the greatest promise of stability. At the outset it was observed that the forms appeared to fall naturally into two groups: (1) those producing both *A* and *B* type spores, and (2) those producing only the *A* type. For a time this grouping seemed to hold until the *B* type spores were discovered for *Phomopsis montanensis* n. sp. of group (2), occurring in scanty numbers.

Another character which appeared to be correlated with the presence or absence of *B* spores was the structure of the inner

pycnidium. This difference in structure of the inner pycnidium was very obvious where the ectostromatic fruit bodies of *Phomopsis occulta* (group 1) and *P. Pseudotsugae* (group 2) occurred on the same substratum (terminal shoots of *Pseudotsuga Douglasii*, amongst the cells of the upper cortex). Forms of group (1) (with the exception of *P. montanensis*), produced a simple fruit body which was unilocular. The simple pycnidium of forms of group (2) (and in *P. montanensis*), on the other hand, was unilocular in the very small, less stromatic fruit bodies, whereas in larger simple pycnidia, several cavities formed throughout the stroma which tended to fuse, forming an irregular, unilocular chamber. This fusion was often incomplete, and a very irregular cavity with septa and partial septa resulted.

The forms of group (2) therefore appeared to resemble both a *Phomopsis* and a *Fusicoccum* but showed the greatest resemblance to the former on account of the pycnidium embedded amongst the cells of the periderm. That part of the pycnidium which became erumpent was dark coloured, carbonaceous, the tissue above the cavities being of varying thickness, and composed of pseudoparenchymatous hyphal cells. The pycnidial walls, the inner cells of which were dilutely coloured, were comparatively much thinner at the sides and on the floor of the fruit body. The spores were borne on sporophores arising from the hymenium lining the irregular cavities; at the base and along the sides of the fruit body, the sporophores looked as if they were originating from the cells of the host itself. This appearance of the simple fruit body, particularly when the cavities had fused to form an irregular unilocular chamber, was quite in keeping with the generally conceived idea of the structure of pycnidia in *Phomopsis*.

It would seem, therefore, that amongst the forms of *Phomopsis* on conifers, which represent only a small number of species, we are probably dealing with forms occurring in a developmental series. For this reason those species may be regarded as transitional in which the *B* type spore does not occur (in one instance referred to, only scantily), and in which the inner plurilocular pycnidium tends to become unilocular. Until the entire life-history of forms of group (2) can be determined, I feel justified in regarding them as within the genus *Phomopsis*, which they appear to resemble most closely. With regard to the establishment of a new genus for group (2), I am quite out of sympathy with tendencies to erect new genera on the basis of each different grouping of characters without a fuller knowledge of the relations and variations of other species of the group.

This becomes more apparent when one compares the development in culture on Leonian's agar of pycnidia of the two groups

(1) and (2) arising from simple and compound primordia. Fundamentally, this development was the same. In both the same type of simple primordium was limited by a brown outer layer. In the non-*B*-spore-forming group (2) the primordium appeared to be smaller in size (less stromatic). In the smallest primordia of both groups, a single cavity formed; in larger primordia cavities were observed to arise at various points which fused to form an irregular cavity with a continuous convoluted hymenium, or fusion was incomplete and the cavities remained separate. In both groups this multilocular fruit body became very noticeable where contiguous primordia fused to form a solid mass of tissue. Archer ((1) p. 23) described this same multiple cavity formation in *Phomopsis coneglanensis*.

The most useful and certain basis for consideration in further classifying forms of groups (1) and (2) was the type, shape and size of the conidia. The form of the spore apices and the presence of peculiarly shaped spores were also morphological characters which were of value in separating the forms into specific groups. Physiological characters, such as culture characteristics, host adaptations and pathogenicity, supplemented morphological data used in segregating species.

Amongst organisms possessing so few morphological characters which can be utilised for species differentiation, the physiological factor becomes important as an aid in morphological differentiation. Mere cultural or biometrical difference alone was not considered sufficient to differentiate a species. Strains showing either of such differences without exhibiting other essential differences can be regarded only as forms of a given species. On the other hand, if several good morphological differences existed, *e.g.* shape and size of spores, presence or absence of different spore types, together with cultural differences, then in accordance with the general tendency for naming fungus species in the past, the forms have been classified provisionally as species; for if it can be shown later that the species described here are merely forms in a series, the connecting links of which have not at present been found and described, the specific status of these organisms should be modified in accordance with their natural relationships.

Dichotomous key to the species of *Phomopsis* on conifers.

Pycnidia ectostromatic or formed in connection with a perithecial entostroma, simple or compound, black, carbonaceous, variable in size, subspherical, cone-shaped or truncate with a flattened base, seated upon and incorporated with the cells of the outer cortex, becoming semi-erumpent; fruit bodies closed,

with a definite ostiole, or breaking open irregularly: inner pycnidium in some with a unilocular cavity, tending to form in one plane, as a lens-shaped, subspherical or conical chamber with a pseudoparenchymatous buffer layer above; or cavity irregular, with protrusions from the walls, tending to become plurilocular; in others, the inner pycnidium with one to several small subspherical chambers formed above each other occupying the greater portion of the inner structure and tending to fuse to form an irregular unilocular cavity with partial or complete septa; hymenium irregularly convoluted, lining the cavity; compound pycnidia, formed by the fusion of adjacent primordia, cavities fusing in one plane to form an irregular plurilocular cavity, or tuberculate, with numerous subglobose chambers. Spores of three types, *A*, *B*, and intermediate; *A* and *B* types generally occurring together, occasionally only the *A* type produced; *A* spores, unicellular, hyaline, oblong, ovate, elliptic to fusoid, with obtuse, subacute or acute extremities, commonly with two guttules; *B* spores, unicellular, hyaline, filamentous, straight, arcuate or hamate, with numerous minute guttules; intermediate spores intergrading between the *A* and *B* spores. Sporophores variable in size, abbreviated, or long processes, flexuous, subulate, arising from the hymenium lining the chambers. Almost universally the imperfect stage of the *Diaporthe* group. *Phomopsis*

a. Simple pycnidia very stromatic, unilocular, loculus formed in one plane, frequently with protrusions from the side walls with a thickened layer of tissue above

b. Both *A* and *B* type spores present

c. *A* spores generally oblong-elliptic with obtuse extremities, or one extremity acute; *B* spores straight or crooked at one end like a walking-stick; perfect stage, *Diaporthe conorum* (Desm.) Niessl; fourteen coniferous host genera *P. occulta*

cc. *A* spores generally elliptic with subacute extremities; often slightly constricted at the median part of the spore; *B* spores flexuous, tending to become straight; parasite on Cupressaceae *P. juniperovora*

ccc. *A* spores generally fusiform; *B* spores much curved, horseshoe-shaped; hosts, *Pinus*, *Pseudotsuga*, *Picea* *P. conorum*

aa. Simple pycnidia less stromatic; very small pycnidia, unilocular, loculus consisting of a single subspherical chamber; larger pycnidia multilocular, chambers tending to fuse and become unilocular with partial septa; thickened layer of tissue above not so pronounced

b. Both *A* and *B* spores present
c. *A* spores generally oblong-elliptic; *B* spores long-cylindric; slightly curved; only known host, *Abies lasiocarpa* — *P. montanensis*
bb. Only *A* spores present
c. Spores generally oblong-elliptic; small, presence of elongated cylindric *A* spore type not noted; hosts, *Pinus, Abies* — *P. Strobi*
cc. Spores generally elliptic-fusoid
d. Spores small, presence of elongate-cylindric *A* spore type; hosts, *Pseudotsuga, Larix, Cedrus, Sequoia, Abies*; parasite on Douglas fir — *P. Pseudotsugae*
dd. Spores large, fusiform, occasionally with irregularities in shape; only known host, *Abies pectinata* — *P. abietina*
ccc. Spores generally irregular fusiform, large, with protuberances, becoming three or four sided with salient angles; only known host, *Abies grandis* — *P. Boycei*

1. ***Phomopsis occulta*** Trav. in *Flora Ital. Crypt.* I, ii (1906), 221.
Syn. *Phoma occulta* Sacc. *Syll. Fung.* III (1884), 150, et Fuck. *Symb. Nachtr.* III (1875), 23; non *Phoma occulta* Desm. (1849).
Phomopsis Thujae Died. in *Krypt. Fl. Mark Brandenburg*, IX, Pilze, VII (1915), 275.
? *P. Cryptomeriae* Kitajima & Kamei.

The original description of *Phomopsis occulta* was given by Fuckel in 1875 when he described the imperfect stage, which he had observed to be associated with the ascomycetous stage, *Diaporthe occulta* (Fuck.) Nits., on cone scales of *Picea excelsa* in Germany. Saccardo ((42) III, p. 150) merely supplied the name and rather unfortunately, for the specific name *occulta* was already occupied by another member of the genus *Phoma*—*P. occulta* Desm. (1849) on *Phragmites*(7). The combination *Phomopsis occulta* (Sacc.) made by Traverso in 1906 and listed by Diedicke ((8) p. 27) is invalid but the binomial can be retained if it is attributed to Traverso as *Phomopsis occulta* Trav.

The present investigation of *Phomopsis occulta* has shown that the species is the imperfect stage of *Diaporthe conorum* (Desm.) Niessl (= *D. occulta, D. pitya*, Sacc.) and that *P. Thujae* described by Diedicke ((9) p. 275) on dead twigs of *Thuja orientalis* L. is only a form of the older fungus. In 1917 von Höhnel had suggested this relationship when he stated that perhaps

"*P. Thujae*, v. H."* was only a form of *P. occulta* (Sacc.) Trav. or "*P. conorum*, v. H."†. At the same time he recognised the fungus *P. occulta* as occurring on spruce shoots, as well as upon cones. Undoubtedly *P. occulta* has been frequently confused with *P. conorum*, a fungus which does not occur in the life-history of *D. conorum*.

As a result of the investigation of forms of *Phomopsis occulta* the species is now recognised as being widely distributed in Europe and North America on a large number of generic hosts. This investigation was begun in the United States when the identification of a comparatively large number of forms was undertaken, which appeared to be closely related morphologically to *P. juniperovora*, a parasite occurring on the Cupressaceae. Further critical studies showed that with one possible exception,‡ the *Phomopsis* forms placed in an arbitrarily segregated group (18) are now to be considered as forms of *P. occulta*. It would appear therefore that this species is not to be regarded as a fungus new to the United States ((50) p. 139) but one widely distributed in that country on a great variety of conifer hosts.

Examination of Exsiccata.

The pycnidia and spores of *Phomopsis occulta* could not be discovered associated with the specimen of *Diaporthe* (*Valsa*) *occulta*, no. 622, *Fungi rhenani* (1863) distributed by Fuckel (Kew Herb.), though they may be found in other specimens, in which event these must be taken as the type. Undoubtedly, in giving an emended description of *P. occulta*, Traverso was dealing with the same fungus which Fuckel observed in 1875. At that time he stated: "After many years I succeeded in finding the rare pyrenomycete (*Diaporthe occulta* (Fuck.) Nke.), this time in association with numerous spermagonia which occupied the young stromata to be found on the outer surface of the scale, whilst on the covered scale portion, always below, a circumscribed stroma with perithecia occurred."

The following exsiccata have been examined:

No. (?). *Phoma* (*Diaporthe*) *conorum*, cone scales of *Picea excelsa*, col. Lb. (Herb. Sacc., Padua). This fungus is *Phomopsis occulta* (*D. conorum*).

No. 236. *Diaporthe occulta* Nits., cone scales, *Pinus sylvestris*, col. Cooke, Fung. Brit. ed. secundo (Herb. Kew). This specimen contains the imperfect stage *P. occulta*.

* Apparently a misquotation for Died.; Diedicke was the author of this combination.

† Another misquotation (see p. 57).

‡ The form of *Phomopsis* isolated from *Cephalotaxus drupacea* Sieb. & Zucc. degenerated in culture, so that further investigation could not be made. The form will be reported later.

No. 1018. *Phomopsis Thujae* Died. Branches of *Thuja occidentalis* Syd. Mycoth. germ. (Herb. Bot. Garden, Berlin). This fungus is *P. occulta*.

Description of the fungus.

Phomopsis occulta Trav., descr. emend.

Pycnidia ectostromatic, or associated with a perithecial entostroma, simple or compound, partially erumpent; black, carbonaceous, cone-shaped, lenticular, subglobose, or truncate, with or without a definite ostiole; inner pycnidium of the simple fruit body, unilocular, cavity formed in one plane with a thickened layer of pseudoparenchymatous tissue above and with protrusions from the side walls; hymenium lining the cavity

Text-fig. 1. *A* spores.

more or less convoluted, and giving rise to sporophores; compound pycnidium plurilocular, chambers tending to form in one plane and fusing to form an elongate irregular chamber, 0·1–1 × 0·1–0·5 mm. (Pl. I, fig. 1). Spores of three types *A*, *B* and intermediate: *A* type (Text-fig. 1), hyaline, unicellular, generally oblong-elliptical with obtuse extremities, intermixed with occasional spores, drawn out and pointed at one end, acute or subacute, extreme range (300) 5–12·4 × 1·6–3·4μ, commonly

6·2–9·3 × 1·9–3·1μ, with two or three oil drops; *B* type (Text-fig. 2), hyaline, unicellular, filamentous, slightly curved or straight, becoming bent at one end like a walking-stick, ex-

Text-fig. 2. *B* spores.

Text-fig. 3. Intermediate spores.

tremities tapering, acute or subacute, extreme range (162) 15·2–32·4 × 1μ, commonly 20·9–27 × 1μ, with several small guttules; intermediate type (Text-fig. 3), frequent intergrading between the *A* and *B* types, very irregular in shape, attenuated,

approaching the filamentous type, extreme range (80) 8·7–15·5 × 1·2–2·5μ, commonly 9·3–13·3 × 1·2–2·2μ; sporophores (Text-fig. 4) flexuous, subulate with tapering acute or subacute extremities persistent; both *A* and *B* type spores produced on the same type of sporophore; extreme range 5·6–15·8 × 1–2·8μ. Spores exuded in a whitish or yellowish tendril.

The imperfect stage of *Diaporthe conorum* (Desm.) Niessl.

Hab. Widely distributed throughout western Europe on the fallen cones and dead stems of *Picea excelsa* Link, *Cupressus sempervirens* L., *Pinus sylvestris* L., *Thuja* sp., *Abies pectinata* DC., *A. grandis* Lindl. and *Pseudotsuga Douglasii* Carr.; according to

Text-fig. 4. Sporophores.

Diedicke on the dead branches of *Thuja occidentalis* L. (syn *Phomopsis Thujae*) in Germany.

I have collected or identified the fungus on dead parts of branches or trunks of fourteen coniferous host genera in North America and Europe as follows: United States: *Taxus baccata* L., *T. baccata* var. *fastigiata* Loud., *T. cuspidata* Sieb. & Zucc., *Taxodium distichum* (L.) Rich., *Sequoia sempervirens* (Lamb.) Endl., *S. gigantea* Torr., *Cryptomeria japonica* Don., *Larix leptolepis* Murr., *L. europaea* DC., *Pseudotsuga Douglasii* Carr., *P. glauca* Mayr., *Tsuga canadensis* (L.) Carr., *Abies homolepis* Sieb. & Zucc., *A. Veitchii* Murr., *Picea pungens* Engelm., *Juniperus virginiana* Linn., *Cupressus sempervirens* Linn., *Thujopsis dolobrata* Sieb. & Zucc.; Canada (British Columbia): *P. Douglasii*; Great Britain: *P. Douglasii*, *A. pectinata* DC.,

Picea sitchensis Carr., *P. excelsa* Link, *Thuja plicata* Don., *Pinus sylvestris* L., *L. europaea* DC.; Denmark: *P. Douglasii* Carr.; Holland: *P. Douglasii* Carr.; France: *A. pectinata* DC.

In Scotland I have frequently found the fungus associated with frost damage amongst nursery and transplant stock of *P. Douglasii*.

Phomopsis Thujae, *a form of* P. occulta.

The biometrical constants derived from measurements of one hundred spores from specimen No. 1018, *Phomopsis Thujae* Died., Syd. Mycoth. germ., were compared with those of three hundred spores of *P. occulta* on Douglas fir. A significant difference was not obtained, as is shown in Table I. The spore shape was identical. *A* form (one hundred spores measured) of *P. occulta* (No. 43939) isolated from *Thuja plicata* showed very close spore size and shape agreement with Diedicke's fungus; culturally the *Thuja* form agreed with forms of *P. occulta* isolated from Douglas fir.

Table I. *Biometric constants of* P. Thujae *compared with those of* P. occulta.

Population	No. of spores	Length. μ	Standard deviation	Coefficient of variability
P. occulta	300	7·5 ± 0·040	1·016 ± 0·028	13·54 ± 0·380
P. Thujae Ex. 1018	100	7·2 ± 0·052	0·776 ± 0·037	10·77 ± 0·520
		Width.		
P. occulta	300	2·4 ± 0·015	0·380 ± 0·011	15·83 ± 0·447
P. Thujae Ex. 1018	100	2·3 ± 0·022	0·332 ± 0·016	14·42 ± 0·702

Phomopsis Cryptomeriae, *a form of* P. occulta.

Phomopsis Cryptomeriae (28), recently described in Japan, and said to cause a "branch wither" disease of *Cryptomeria japonica*, possibly may be regarded also as a form of *P. occulta*. The spore size ranges given for the fungus are very suggestive—*A* spores, 6·4–8·1 × 2·1–2·5μ, and *B* spores, 28–33·6 × 0·8–1μ. The ranges overlap closely those given by the author for three hundred spores of forms of *P. occulta* on *Pseudotsuga Douglasii*. The *A* spores of the Japanese form are described as oblong with two guttules. Culture study of this Japanese species will be necessary to decide whether it is distinct from *P. occulta*.

2. *Phomopsis juniperovora* Hahn in *Phytopath.* x (1920), p. 249.

Phomopsis juniperovora Hahn, is a widely distributed fungus on nursery seedling and transplant stock of the Cupressaceae in the United States. Artificial inoculation experiments (16) proved

the parasitic nature of this fungus. Up to the present it is not known to occur in Europe, although an intensive search may reveal its presence on the Continent in nurseries where ornamental stock of the Cupressaceae are grown. Unsuccessful search for it has been made in Great Britain.

In 1919, Bottomley reported a preliminary investigation into a disease attacking young *Cupressus* plants in South Africa. The symptoms were identical with those described for *Phomopsis juniperovora* in the United States and attention was called to the close resemblance between the parasites. Several morphological differences were, however, noted; she did not describe *B*, or intermediate spores, and the culture growth characteristics also appeared to be distinct. The South African fungus may possibly be regarded as a physiological form of *P. juniperovora*, though it may be a distinct species.

In my last paper on *Phomopsis juniperovora* ((18) p. 901) I stated, "Single spore cultures from red cedar (*Juniperus*) were observed which produced only a bare suggestion of the colour (orange-rufous), or lacked it entirely. These strains were classed as *P. juniperovora*, despite the abnormality in the colour character, on the basis of their origin on a cedar host in a locality where the typical colour-producing fungus was known to occur." I am now in a position to report that there does seem to be a tendency for certain forms of *P. juniperovora* to produce the characteristic orange-rufous colour only in a slight degree. Such for example was so in strain No. 43968, isolated from diseased *Juniperus virginiana* from Rhode Island. This strain, however, was fully capable of producing the flaming orange crystals. The forms referred to, in which the orange colour was lacking entirely, were thus very closely related with *P. occulta*. It would therefore be interesting to know if Bottomley's *Phomopsis* species on *Cupressus* might not possibly be a physiological form of *P. occulta* parasitic in that particular locality. *P. juniperovora* itself appears to be confined to the Cupressaceae.

Description of the fungus.

Phomopsis juniperovora Hahn*.

Pycnidia ectostromatic, not associated with a perithecial entostroma, simple or compound, partially erumpent, black, carbonaceous, cone-shaped, lenticular, subglobose or truncate, with or without a definite ostiole; inner pycnidium of simple

* Descriptions of *Phomopsis juniperovora* and *P. Strobi* have been published, together with recent emended descriptions of *P. Pseudotsugae*, *P. abietina* and *P. conorum*. These descriptions are repeated here with certain slight modifications. These changes are necessary on account of additional information secured by a further study of the species.

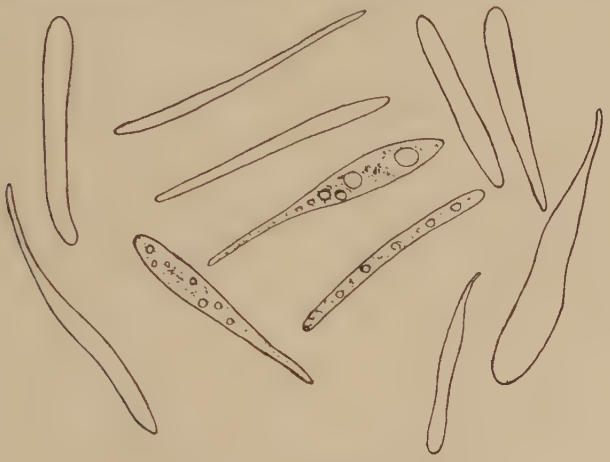
fruit body, unilocular, cavity formed in one plane, with a thickened layer of pseudoparenchymatous tissue above, frequently with protrusions from the side walls; the hymenium lining the

Text-fig. 5. *A* spores.

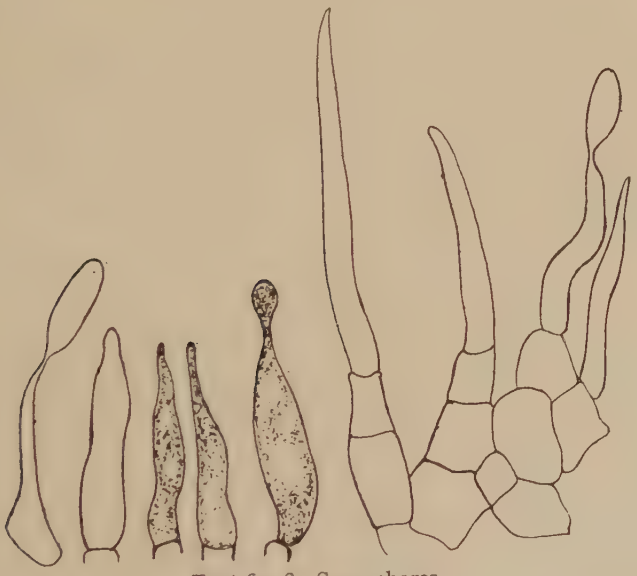
Text-fig. 6. *B* spores.

cavity which gives rise to the sporophores, more or less convoluted; compound pycnidium, multilocular, chambers tending to form in one plane and fusing to produce an elongate, irregular

chamber; 0·1–0·6 × 0·1–0·4 mm. Spores of three types, *A*, *B* and intermediate; *A* type, hyaline, unicellular, typically



Text-fig. 7. Intermediate spores.



Text-fig. 8. Sporophores.

ellipsoid with subacute extremities and with a "pinching in," or narrowing, at the median part of the spore, symmetrical or asymmetrical, occasionally oblong-elliptic with obtuse ex-

tremities, or elliptic-fusoid, extreme range (100) 5·6–12 × 1·9–3·5μ, commonly 7·5–10 × 2·2–2·8μ, biguttulate (Text-fig. 5); *B* type, hyaline, unicellular, filamentous, only slightly curved, flexuous, tending to become straight, not pronouncedly hooked or bent at one end as in *P. occulta*, extremities tapering, one frequently obtuse; extreme range 17·1–34 × 1μ, commonly 20·2–26·9 × 1μ; with several minute guttules (Text-fig. 6); intermediate type, occurring infrequently, intergrading between the *A* and *B* types, very irregular in shape, attenuated, approaching the filamentous type, extreme range (20) 9·9–17·7 × 1·6–2·5μ (Text-fig. 7); sporophores, subulate, persistent, both *A* and *B* type spores produced on the same type of sporophore, extreme range 5·9–25·7 × 1–3·1μ, commonly 11·2–14·3 × 1–2·5μ (Text-fig. 8). Spores exuded in a whitish or yellowish tendril.

Perfect stage unknown.

Hab. Widely distributed in the United States on species of the Cupressaceae*. An extensive host list has been recently published (18).

Comparison of Phomopsis juniperovora *and* P. occulta.

At first glance it must be admitted that *Phomopsis juniperovora* and *P. occulta* resemble each other very closely. It was not until they had been studied culturally, and certain morphological differences separating the species detected, that they could be distinguished; for both species were found on hosts amongst the Cupressaceae, upon which the former fungus is known to be parasitic.

Table II. *Biometric constants of* A *spores of* P. juniperovora *compared with* P. occulta (*two generic host forms*).

Population	No. of spores	Length. μ	Standard deviation	Coefficient of variability
Phomopsis juniperovora	100	8·7 ± 0·066	0·984 ± 0·047	11·31 ± 0·547
P. occulta[1]	300	7·5 ± 0·040	1·016 ± 0·028	13·54 ± 0·380
P. occulta[2]	100	7·2 ± 0·052	0·776 ± 0·037	10·77 ± 0·520
		Width.		
Phomopsis juniperovora	100	2·5 ± 0·025	0·364 ± 0·017	14·56 ± 0·709
P. occulta	300	2·4 ± 0·015	0·380 ± 0·011	15·83 ± 0·447
P. occulta	100	2·3 ± 0·022	0·332 ± 0·016	14·42 ± 0·702

[1] Douglas fir forms. [2] *Thuja* form.

* Under conditions of artificial inoculation experiments, positive results (18) were obtained with *Phomopsis juniperovora* on *Pseudotsuga Douglasii* and *Larix europaea*; negative results on *Pinus* (six species) and *Picea* (three species).

The spore size ranges of the two species closely overlap in their range variation, in fact so closely, that to separate them satisfactorily the measurements must be treated biometrically. Such a comparison of biometrical constants is given in Table II, where spore populations of the species *Phomopsis juniperovora* (ten forms on *Juniperus*) are compared with the species *P. occulta* (ten forms on Douglas fir) and with the same species on *Thuja* (one form). A significant difference was obtained only in regard to spore length.

3. ***Phomopsis conorum*** (Sacc.) Died. in *Ann. Mycol.* IX (1911), p. 22.

Syn. *Phoma conorum* Sacc. in *Mich.* II (1882), p. 615, and *Syll. Fung.* III (1884), p. 150.

Septoria conorum (Sacc.) Oud. in *Ned. Kr. Ark.* Ser. 3, II (1900), p. 270.

Phomopsis conorum Died. var. *naviculispora* Trav. in *Bull. Soc. Fl. Valdotaine*, VIII (1912), p. 27.

Phomopsis pitya Lind, pro parte Danish Fungi in Herb. E. Rostrup, 1913, non *Phoma pitya* Sacc.

Phomopsis conorum (Sacc.) Died. was originally described in 1882 as *Phoma conorum* (*Diaporthe conorum*) on the cone scales of spruce. The description was very meagre and apparently was based on two specimens collected by Mlle Libert (Lb. 291, 295). In 1901, Saccardo ((42) III, p. 150) restated this description and gave both Germany and France as the habitat of the fungus. Diedicke ((8) p. 22) in his discussion of the genus *Phomopsis* listed the new combination, *Phomopsis conorum* (Sacc.), but he did not give further morphological detail regarding the fungus. Later, in 1913, Saccardo ((42) XXII, p. 903) gave an amended description of this organism.

In 1917, von Höhnel had suggested that *Phomopsis Thujae* Died. was only a form of *P. occulta* (Sacc.) Trav. or "*P. conorum* (Sacc.) v. H." We now know that *P. Thujae* is to be regarded as a form of *P. occulta*. Evidently "von Höhnel" as an authority for the combination *P. conorum* is a slip.

Phomopsis conorum and *P. occulta*, both species which have been confused by mycologists, are distinct, and readily distinguishable both morphologically and physiologically. Both species occur on all plant parts—cones, stems, leaves and trunks. In the minds of the older mycologists there appears to have been a tendency to segregate fungus forms on cones from those occurring on conifer stems. Such a conception would needlessly tend to increase the species number.

I have recently shown (19) that the well-known fungus *Phoma pitya* discussed by Rostrup (40) and figured in his *Plantepatologi*

as an attributed parasite causing die-back of the terminals of Douglas fir and other conifers, and later regarded by Lind as *Phomopsis pitya* (Sacc.), is no other than *P. conorum* (in part, for other fungus species were found among Rostrup's collections of *P. pitya*). It is perhaps to be regretted that an organism should bear the specific name *conorum*, when it is also stem inhabiting, and furthermore, when it does not occur within the life-history of *Diaporthe conorum*.

Examination of Exsiccata.

The following exsiccata have been examined:

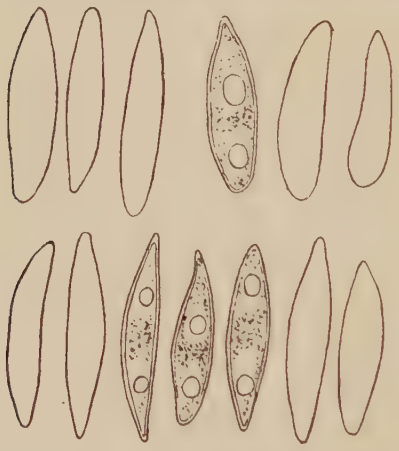
No. 1727. *Phoma* (*Diaporthe*) *conorum* Sacc., on spruce cone scales, Reliq. Lb. (Herb. Brussels). This fungus is *Phomopsis conorum*; not *D. conorum*.

Phoma (*Diap.*) *conorum* Sacc., on spruce cone scales, coll. Lb. (Herb. Sacc., Padua). This fungus is *P. occulta* (*D. conorum*).

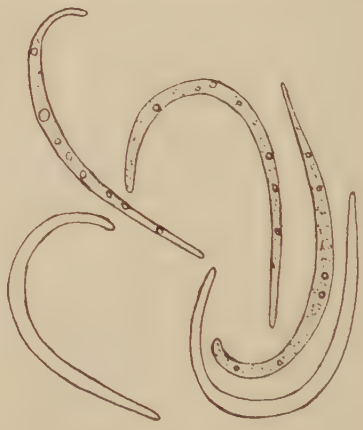
Description of the fungus.

Phomopsis conorum (Sacc.) Died.

Pycnidia ectostromatic, not associated with a perithecial entostroma, simple or compound, embedded, partially erumpent; black carbonaceous, cone-shaped, lenticular, subglobose or



Text-fig. 9. *A* spores.



Text-fig. 10. *B* spores.

truncate with or without a definite ostiole; inner pycnidium of simple fruit body, unilocular, cavity formed in one plane with a thickened layer of pseudoparenchymatous tissue above, and with protrusions from the side walls and base of the fruit body, hymenium lining the cavity more or less convoluted giving rise

to sporophores; compound pycnidium, multilocular, chambers also tending to form and fuse in one plane; 0·1–2 × 0·1–0·8 mm. (Pl. I, fig. 2). Spores of three types, *A*, *B* and intermediate; *A*

Text-fig. 11. Intermediate spores.

Text-fig. 12. *A* sporophores.

type, hyaline, unicellular, generally spindle-shaped with acute or subacute, gently rounded extremities, rarely elliptic, extreme range (420) 6·2–14·6 × 2·5–4·7μ, commonly 7·5–12·4 × 2·5–3·7μ, with two, or occasionally three guttules (Text-fig. 9); *B*

type, hyaline, unicellular, filamentous, pronouncedly curved, hamate, horseshoe-shaped, rarely straight, extreme range (154) 10–34·4 × 1μ, commonly 20·2–24·1 × 1μ, with several minute guttules (Text-fig. 10); intermediate spores rare, intergrading between the *A* and *B* spores, very irregular in shape, attenuated, approaching the filamentous type, extreme range (50) 11·8–18 × 1·2–2·5μ, commonly 13–15·5 × 1·6–2·2μ (Text-fig. 11); sporophores, persistent, flexuous, subulate, with tapering acute

Text-fig. 13. *B* sporophores.

or subacute extremities, both *A* and *B* type spores produced on the same type of sporophore, extreme range 5·6–21·4 × 1–2·5μ (Text-figs. 12, 13). Spores exuded in a whitish or yellowish tendril.

Perfect stage unknown; not *Diaporthe conorum*.

Hab. According to Saccardo on the cone scales of *Picea excelsa* in France and Germany; according to Traverso on the same host in Italy; the fungus was identified by me among collections of fungi on *Pseudotsuga Douglasii* and *Abies balsamea* made in Denmark by Rostrup (19); Lind (*Danish Fungi*, p. 421)

listed the fungus on cone scales of *P. excelsa* in Denmark (Seeland).

The fungus has been collected or identified by me on the following: in Scotland—on dead parts of living nursery plants of *Pseudotsuga Douglasii* and *Picea sitchensis*; on trunk of dead tree of *Pinus Strobus* L.; on fallen cones of *Picea excelsa*; in England—on frosted plantation stock of *P. sitchensis*; in Holland—on dead parts of nursery transplant stock of *P. Douglasii*.

4. *Phomopsis montanensis* n. sp.

In 1927, material of dead branches of *Abies grandis* Lindl. and *A. lasiocarpa* Nutt. collected by Mr C. R. Stillinger in Montana was sent by Dr Boyce for identification. Stillinger reported that dead flags associated with the fungus were abundant in all age classes of the alpine fir, and that sometimes 25 per cent. of the branches were killed. A diagnosis of this material showed that *Phomopsis Boycei* (see p. 72) occurred on the diseased branches of the lowland fir, whereas a *Phomopsis* species, morphologically distinct, was discovered on the alpine fir. This species is here provisionally described as new.

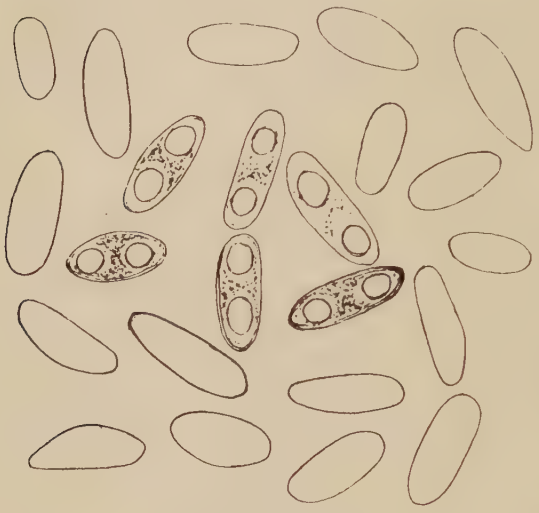
Description of the fungus.

Phomopsis montanensis n. sp.

Pycnidia ectostromatic, embedded, arising within and seated upon the cells of the upper cortical tissue, amongst whose cells the fruit body is more or less incorporated; partially erumpent, simple or compound; black, carbonaceous; cone-shaped, lenticular, subglobose or truncate, breaking open with an irregular orifice or somewhat ostiolate; inner pycnidium of simple fruit body, unilocular in the smaller bodies, cavity subspherical or elliptical with a thickened layer of pseudoparenchymatous tissue above, not heavily developed, larger simple pycnidia at first plurilocular, cavities forming above each other and tending to fuse producing an irregular cavity with partial septa, lined with a convoluted hymenium; compound pycnidia multilocular, with numerous chambers; 0·1–0·5 × 0·1–0·4 mm. (Pl. II, figs. 2, 3); spores of two types, *A* and *B*; *A* type, hyaline, unicellular, generally oblong or elliptical, or ovate with obtuse extremities, extreme range (100) 5·3–8·1 × 2·2–3·4μ, commonly 6–7·8 × 2·5–3·4μ (av. 6·9–2·8μ), with two guttules (Text-fig. 14); *B* type, hyaline, unicellular, filamentous, cylindrical slightly curved or almost straight, occurring rarely, extreme range (20) 9·3–11·8 × 0·9μ, with several minute guttules (Text-fig. 15); sporophores, short, delicate, subulate, extreme range (20) 4·7–11·1 × 0·9–3·1μ

(Text-figs. 16, 17); spores exuded in a whitish or yellowish tendril.

The perfect stage is unknown.



Text-fig. 14. *A* spores.

Text-fig. 17. *B* sporophores.

Text-fig. 15. *B* spores.

Text-fig. 16. *A* sporophores.

Hab. On dead branches and twigs of *Abies lasiocarpa* in Montana. Type specimen, No. 43987, collected by C. R. Stillinger, August 24th, 1927, Belton, Mont.

Phomopsis montanensis n. sp.

Pycnidiis discretis vel aggregatis, ab initio subepidermicis denique erumpentibus; carbonaceis, lenticularibus, conoideis,

truncatis, vel subglobosis, ostiolis paulo pertusis, vel deficientibus, contextu heterogeneo praeditis, matricibus fuligineis supra cavitates sporiferas incrassatulis; pycnidiis parvis, majoribus multilocularibus vel per dissepimentum disruptionem unilocularibus, ceteris unilocularibus; 0·1–0·5 × 0·1–0·4 mm. Sporulis dimorphis: *A* sporulis, hyalinis, continuis, oblongis vel ovatis, guttulatis, (100) 5·3–8·1 × 2·2–3·4 μ, vulgo, 6–7·8 × 2·5–3·4 μ; *B* sporulis filiformibus, leviter curvatis, guttulatis minutis, (20) 9·3–11·8 × 0·9 μ; basidiis continuis, subulatis, brevibus, tenuibus, 4·7–11·1 × 0·9–3·1 μ.

Hab. In ramis emortuis *Abietis lasiocarpae* Nutt. in America boreali (Montana), August, 1927.

Comparison of Phomopsis montanensis *with* P. Pseudotsugae *and* P. Strobi.

A preliminary examination of *Phomopsis montanensis* showed it to be distinct from *P. Boycei* on *Abies grandis*. It appeared to most closely resemble *P. Pseudotsugae* and *P. Strobi*. The culture growth characteristics were distinct, however, differentiating the organism physiologically from both of these species.

A biometrical study of a hundred spores of the type specimen was made, the constants of which are given in Table III in comparison with those of *P. Pseudotsugae* and *P. Strobi*. A significant difference is indicated between spore populations of *P. montanensis* and *P. Strobi*, but not between it and *P. Pseudotsugae*. Although a significant difference did not exist between *P. montanensis* and *P. Pseudotsugae*, other morphological differences tended to separate the Douglas fir organism as a distinct species; *B* spores which were described for the fungus on *Abies lasiocarpa* are not known to occur in *P. Pseudotsugae*.

Table III. *Biometric constants of* P. Pseudotsugae, P. Strobi (*type*), P. Strobi (Abies pectinata *Italy*), *and* P. montanensis, *compared*.

Population	No. of spores	Length. μ	Standard deviation	Coefficient of variability
P. montanensis (type)	100	6·9 ± 0·052	0·767 ± 0·037	11·12 ± 0·537
P. Pseudotsugae	200	6·7 ± 0·074	1·56 ± 0·053	23·29 ± 0·827
P. Strobi (type)	100	5·8 ± 0·033	4·88 ± 0·023	8·41 ± 0·404
P. Strobi (*A. pectinata* Italy Petri col.)	100	5·8 ± 0·051	7·61 ± 0·036	13·12 ± 0·636
		Width.		
P. montanensis (type)	100	2·9 ± 0·020	0·302 ± 0·014	10·40 ± 0·501
P. Pseudotsugae	200	2·6 ± 0·022	0·466 ± 0·016	17·93 ± 0·624
P. Strobi (type)	100	2·3 ± 0·023	0·335 ± 0·016	14·56 ± 0·709
P. Strobi (Italy)	100	2·3 ± 0·033	0·487 ± 0·023	21·17 ± 1·054

5. ***Phomopsis Strobi*** Syd. in *Ann. Myc.* XX (1922), p. 204.

Phomopsis Strobi was described by Sydow from material collected by Weir on limbs of *Pinus Strobus* in the United States (Maine, 1918). It occurred in association with *Peridermium Strobi* Kleb. According to Sydow: "The fungus can evidently be regarded only as a *Phomopsis*. It differs essentially from the typical form of the genus only by the delicate conidiophores. We were not able to identify the form with other of the numerous forms described on conifers. *Phoma Pini* Cooke & Hark. (Sacc. *Syll. Fung.* III, p. 73) appears to be another fungus."

Description of the fungus.

Phomopsis Strobi Syd.

Pycnidia ectostromatic, simple or compound, partially erumpent, black, carbonaceous, cone-shaped, subglobose, breaking open irregularly at the apex; inner pycnidium of simple fruit body, unilocular, cavity more or less spherical or elliptical without a heavy development of pseudoparenchymatous tissue above, or in larger simple pycnidia, plurilocular with several fully formed or incomplete chambers of various sizes and shapes

Text-fig. 18. *A* spores.

Text-fig. 19. Sporophores.

formed above each other, which tend to fuse, becoming irregularly unilocular with partial septa and with a convoluted hymenium; walls thin at the sides and on the floor of the pycnidium, so that the sporophores appear to rise from the cells of the host itself, due to the embedded nature of the fruiting body, walls composed of hyaline and yellowish coloured elongated cells, 12–15μ thick; compound pycnidia, multilocular, with many chambers; 0·1–0·6 × 0·1–0·4 mm. Spores of one type, *A* type, hyaline, unicellular, oblong-elliptic, but varying to elliptic-fusoid, extremities obtuse, symmetrical or asymmetrical, ex-

treme range (100) 4·7–7·1 × 1·9-3·1μ, commonly 5–6·5 × 1·9–2·8μ, with two guttules (Text-fig. 18); sporophores (Text-fig. 19) very short, delicate, subulate, 4·5–8·1 (10) × 0·6–1·2μ.

Perfect stage unknown.

Hab. On limbs of *Pinus Strobus* Linn. in the United States (Maine). Specimens of *Phomopsis* on *Pinus montana* Mill. and *P. Strobus* collected by Rostrup in Denmark (1884) and identified by him as *Phoma pitya*, were examined (18) and found to be forms of *P. Strobi*.

Comparison of Phomopsis Strobi *with* P. Pseudotsugae, *and with forms on* Abies *and* Pinus *in Europe.*

Only one form of *Phomopsis Strobi* (type No. 10898, Herb. Syd. Berlin) was studied intensively with regard to spore size. It was found that the size range of the Danish specimens collected by Rostrup and identified by him as *Phoma pitya* (18) was within that of the spore range of the type. The shape of the spores of these collections on *Pinus montana* and *P. Strobus* agreed with that of Sydow's type.

Text-fig. 20. *A* spores, Petri's *Phomopsis* sp.

Phomopsis Strobi was also compared with a form of *Phomopsis* on *Abies pectinata* collected by Professor Petri in Italy, cultures of which were received from him for comparison with forms of *P. abietina* from the same host. Culturally Petri's *Phomopsis* differed from all the *Phomopsis* forms investigated in this paper; morphologically (Text-figs. 20, 21) it appeared to most closely resemble *P. Strobi* and *P. Pseudotsugae*. A comparison was made of the biometrical constants of spores of the following: *P. Strobi* (type), *P. Pseudotsugae* and the culture form of the Italian *Phomopsis* on oat agar. This comparison which is presented in Table IV shows that the only significant difference lies between

the constants determined for length of both *Phomopsis* sp. and *P. Strobi*, and *P. Pseudotsugae*. Until it is possible to obtain fresh material of *P. Strobi* for culture study, it is assumed that *P. Strobi* and the *Phomopsis* species obtained from Petri are probably identical, or at least physiological forms of the same

Text-fig. 21. Sporophores, Petri's *Phomopsis* sp.

species. If such an assumption be true, then *P. Strobi*, which is distinct culturally from *P. Pseudotsugae*, and which shows other morphological differences in the size and the shape of the pycnidiospores, must be regarded as a distinct species. It is admitted, however, that the relation between *P. Pseudotsugae* and *P. Strobi* is very close.

Table IV. *Biometrical constants of* P. Strobi, Phomopsis *sp.* (Petri) *and* P. Pseudotsugae, *compared.*

Population	No. of spores	Length. μ	Standard deviation	Coefficient of variability
P. Strobi (type)	100	5·8 ± 0·033	0·488 ± 0·023	8·41 ± 0·404
Phomopsis sp. (Petri)	100	5·8 ± 0·051	0·761 ± 0·036	13·12 ± 0·636
P. Pseudotsugae	200	6·7 ± 0·074	1·56 ± 0·053	23·29 ± 0·827
		Width.		
P. Strobi (type)	100	2·3 ± 0·023	0·335 ± 0·016	14·56 ± 0·709
Phomopsis sp. (Petri)	100	2·3 ± 0·033	0·487 ± 0·023	21·17 ± 1·054
P. Pseudotsugae	200	2·6 ± 0·022	0·466 ± 0·016	17·93 ± 0·624

6. ***Phomopsis Pseudotsugae*** Wilson in *Trans. Bot. Soc. Edin.*, XXVIII (1920), p. 47; *Forestry Comm. Bull.* VI (1925), p. 9; *Trans. Brit. Myc. Soc.* XIII (1928), p. 273.

Phomopsis Pseudotsugae was first described by Wilson in 1920, and later more fully in 1925. He attributed a die-back and canker disease of the Douglas fir and other conifers to this organism, the pathological symptoms of which he discussed and figured in detail in the later publication.

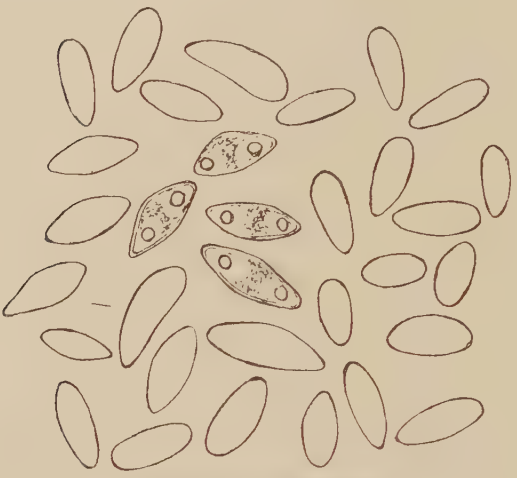
The relationships of *Phomopsis Pseudotsugae* have been stated both by Wilson (62) and by Boyce (3). On account of the confusion in the literature due to a lack of knowledge concerning the actual identity of *Phoma pitya* Sacc. and *Phoma abietina* Hart., a state of affairs had been reached wherein the names *P. pitya* and *P. abietina* were regarded by some authorities as interchangeable and were used indiscriminately. At the same time *P. Pseudotsugae* was also being confused with these two species. To clear up the situation, an investigation of the type specimen of *P. pitya* was undertaken, together with that of authentic specimens of *P. abietina*. The results of this research, which proved the separate identity of these three organisms, were published recently by Wilson and Hahn (63, 19).

Phomopsis Pseudotsugae appears to be a good species. It seems to be most closely related to *P. Strobi*, but several morphological, as well as probable physiological differences separate the two. *P. Pseudotsugae* is known only in Europe. Whether it exists in America on the Douglas fir is problematical. Considering the large amount of importation of conifers from Europe, which are hosts for the species, it would not be surprising if the organism were found there eventually.

Description of the fungus.

Phomopsis Pseudotsugae Wilson.

Pycnidia ectostromatic, closed, simple or compound, embedded, partially erumpent; black, carbonaceous; lenticular, obpyriform, subglobose, with or without a definite ostiole, or breaking open irregularly; inner pycnidium of very small simple fruit bodies, unilocular, cavity subspherical or elliptical, or in larger simple bodies, plurilocular, cavities tending to fuse forming an irregular unilocular cavity lined with a convoluted hymenium from which the sporophores arise; walls thin at the sides and on the floor of the pycnidium, composed of yellowish and hyaline elongated cells; tissue above the cavities not strongly developed, pseudoparenchymatous, olivaceous; large compound pycnidia, with many chambers; 0·1–1 × 0·1–0·4 mm.; (Pl. I, fig. 3; Pl. II, fig. 1); spores of one type only, *A* type, hyaline, unicellular typically elliptic-fusoid, but varying in some to ovate or oblong, with subacute or obtuse extremities (Text-fig. 22), occasional longish spores, elongate-elliptical, or cylindrical, with obtuse or subacute extremities (Text-fig. 23); extreme range (210) 4·7–12·4 × 1·9–3·4μ, commonly 5·3–9 × 2·2–3·1μ (av. 6·7 × 2·6μ), occasionally with two guttules; sporophores short, delicate, subulate, 4·7–10·5 × 1–2·5μ (Text-fig. 24). Spores exuded in a whitish tendril or droplet, or in



Text-fig. 22. *A* spores.

Text-fig. 23. Elongate *A* spores.

Text-fig. 24. Sporophores.

compound pycnidia, several tendrils emerging from different parts of the same fruit body.

Perfect stage unknown; not *Diaporthe conorum* (= *D. pitya*).

Hab. On branches, trunks, leaves of *Pseudotsuga Douglasii* in Great Britain, Ireland, Norway, Sweden, Denmark and Holland; also on branches of *P. glauca, Larix europaea, L. leptolepis, L. Sibirica* Ledeb., *Abies pectinata, Cedrus atlantica* Manetti, *C. Deodara* Loud. and *Sequoia gigantea.*

The parasitism of *P. Pseudotsugae* has been proved upon Douglas fir, larch and *Cedrus.*

7. ***Phomopsis abietina*** (Hartig) Wils. & Hahn in *Brit. Mycol. Soc.* XIII (1928), p. 272.

Syn. *Phoma abietina* Hartig. *Lehrbuch d. Baumkr.* ed. 2 (1889), p. 124.

Dothiorella pitya Prill. & Delacr. in *Bull. Soc. Myc. Fr.* VI (1890), p. 174.

Fusicoccum abietinum Prill. & Delacr. *Tom. cit.* p. 98.

In his original description (1889) of the fungus associated with the classical "Einschnürungskrankheit" of the silver fir (*Abies pectinata*) Hartig provisionally described the organism as *Phoma abietina.* A year later Prillieux and Delacroix (34) in France, placed the fungus in the genus *Fusicoccum,* as *F. abietinum* (Hart.). They gave a full description of the fungus, emphasising the multilocular nature of the fruit body. Originally they had regarded this fungus as *Dothiorella pitya* Sacc. (33), but upon a comparison with the type specimen of Saccardo's fungus (*Fungi Veneti,* Ser. IV, p. 5; Sacc. *Syll. Fung.* III, 241) decided they were dealing with another fungus.

In 1921, Grove made the new combination *Phomopsis abietina* (Hart.), describing the organism from specimens of *Phomopsis* on Douglas fir from Perthshire, Scotland. The identity of *Phoma abietina* has been further investigated, and the results of an intensive study of the species have been recently published by Wilson and Hahn (63). The combination *Phomopsis abietina* Grove was apparently not based upon the fungus described by Hartig and by Prillieux and Delacroix. Accordingly Wilson and Hahn made the combination *P. abietina* (Hart.) which had a significance distinct from that used by Grove, and in doing so referred only to the fungus described by the German and French authors on silver fir.

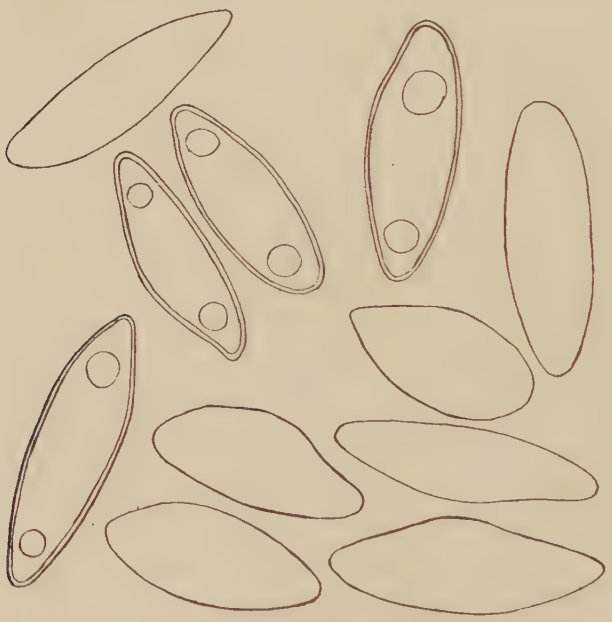
It is indeed interesting to note that typical *Phomopsis abietina* has not been recorded definitely outside Germany and France. I have searched for it and the characteristic symptomatology of the disease in Great Britain and in Scandinavia without success. Stevenson ((50) p. 3) listed the fungus from the

United States on *Abies Veitchii* in Ohio, but this specimen proves to be *P. occulta*. Doidge (10) reported *P. abietina* on *Pinus* spp. and *Cupressus* sp. from South Africa. The original account (2) would suggest *P. occulta* and possibly *P. juniperovora*.

Description of the fungus.

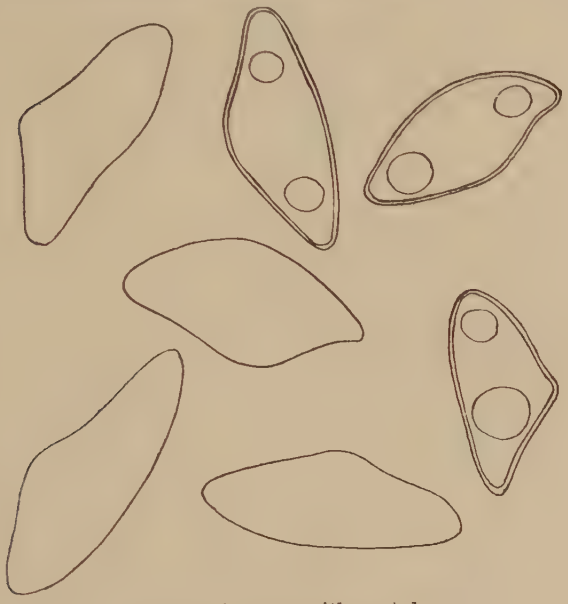
Phomopsis abietina (Hart.) Wilson & Hahn.

Pycnidia ectostromatic, embedded, simple or compound, partially erumpent; black, carbonaceous, cone-shaped, lenticular, truncate or subglobose, with or without an ostiole, inner pycnidium a very small simple fruit body, unilocular, or in larger pycnidia plurilocular with several small cavities formed above each other, chambers tending to fuse and forming an irregular unilocular cavity, with a convoluted hymenium which



Text-fig. 25. *A* spores.

gives rise to the sporophores; tissue overlying the cavities dark, fuliginous, pseudoparenchymatous, variable in thickness; walls at the sides and on the floor of the fruit bodies comparatively thin; compound pycnidia, multilocular with numerous chambers, dehiscing at several openings; 0·08–0·5 × 0·05–0·4 mm. (Pl. III, figs. 1, 2); spores of one type only, *A* type, hyaline, unicellular, typically fusoid-elliptic (spindle-shaped), with acute or subacute



Text-fig. 26. *A* spores with protuberances.

Text-fig. 27. Sporophores.

extremities (Text-fig. 25), symmetrical or asymmetrical, spores infrequently irregular with protuberances (Text-fig. 26), extreme range (100) 8·4–14·9 × 3·4–5·6μ, commonly 10·9–14 × 4–5·3μ, with one, generally two, occasionally three guttules;

sporophores stout, subulate, persistent with tapering acute or subacute extremities (Text-fig. 27), extreme range 6·7–13 × 1–3·4μ. Spores exuded in a whitish tendril or globular mass.

The perfect stage is unknown.

Hab. Only on the smaller branches of *Abies pectinata* on the Continent in Germany and France.

8. *Phomopsis Boycei* n. sp.

In 1926 Dr J. S. Boyce sent specimens of lowland fir (*Abies grandis*) which he had collected in the vicinity of Clarkia, Idaho, U.S.A., and reported that cankers on dead branches were associated with a fungus which macroscopically resembled a *Phoma* or a *Phomopsis*. He suggested that the organism might be *Phomopsis* (*Phoma*) *abietina*, which is commonly reported from continental Europe as killing branches of the silver fir. The attributed Idaho parasite was observed to kill many branches.

The symptomatology of the Idaho canker on lowland fir was identical with the well-known "Einschnürungskrankheit" of the silver fir described and figured by Hartig. The *Phomopsis* species, according to Boyce, affected only the smaller branches, usually those not exceeding one-half inch in thickness. He never observed it on the main stem, except occasionally killing the leader of small trees. In this respect it is interesting to note that Hartig (23) and Mer (31, 32) described a similar occurrence of *Phoma abietina* only on the small branches of silver fir.

A critical examination of the fungus showed it to be closely akin to Hartig's *Phoma abietina*. Difficulty was experienced in placing it definitely in the *Phomopsis* group because of the extremely irregular, angular appearance of the spores. The literature has been searched for descriptions or figures of spores belonging to species amongst the Fungi imperfecti with pycnidiospores similar to those produced by the Idaho fungus. None were found until Mr E. W. Mason of the Imperial Bureau of Mycology, called the writer's attention to the spores of *Vanderystiella leopoldvilleana* P. Henn (60), one of the Melanconiaceae, which was described and figured as being "fusoideo-tetraedricis, acutis."

In the preceding section spores with protuberances were discussed as occurring infrequently on *Phomopsis abietina*. In the Idaho *Phomopsis*, the angular spore type was predominant, and not the spindle-shaped form as in *P. abietina*. Moreover, on account of biometrical (Table V) and cultural differences between the two forms, the Idaho fungus is regarded as not only morphologically but physiologically distinct from the European species. It is therefore described provisionally as a new species,

P. Boycei, in honour of its discoverer, Dr J. S. Boyce, of the Forest Service, United States Department of Agriculture.

Table V. *Biometrical constants of* P. Boycei *and* P. abietina *compared.*

Population	No. of spores	Length. μ	Standard deviation	Coefficient of variability
P. Boycei	100	11·2 ± 0·061	0·897 ± 0·043	8·01 ± 0·385
P. abietina	100	12·3 ± 0·085	1·252 ± 0·060	10·18 ± 0·491
		Width.		
P. Boycei	100	5·9 ± 0·054	0·793 ± 0·038	13·43 ± 0·652
P. abietina	100	4·5 ± 0·034	0·508 ± 0·024	11·28 ± 0·545

Description of the fungus.

Phomopsis Boycei n. sp.

Pycnidia ectostromatic, simple or compound, embedded, arising within and seated upon the cells of the cortical tissue, amongst whose cells the fruit body is more or less incorporated, partially erumpent; black, carbonaceous, with the ostiole

Text-fig. 28. *A* spores.

slightly developed or breaking open irregularly; cone-shaped or subglobose; inner pycnidium of simple fruit body, unilocular, cavity subspherical or elliptical with a superimposed layer of dark, fuliginous pseudoparenchymatous tissue above, not

heavily developed, larger pycnidia plurilocular, the chambers fusing irregularly and tending to form a unilocular cavity lined with a convoluted hymenium; compound pycnidia, distinctly multilocular; 0·1–0·5 × 0·1–0·4 mm. (Pl. III, fig. 3); spores of one type, *A* type, hyaline, unicellular, irregularly fusoid with salient angles so that the spores become three or four-sided; rarely symmetrical, elliptic fusoid, with acute or subacute extremities, extreme range (100) 9–13 × 4–7·8μ, commonly 9·9–12·4 × 5–6·8μ (av. 11·1 × 5·9μ)*, with one, two or three guttules (Text-fig. 28); sporophores short, stout, subulate, with tapering extremities, 5–9·9 × 1–2·5μ (Text-fig. 29). Spores

Text-fig. 29. Sporophores.

exuded in a whitish tendril or droplet; several tendrils emerging from a compound fruit body.

Perfect stage unknown.

Hab. Type, No. 40373, coll. J. S. Boyce, on *Abies grandis*, Clarkia, Shoshone Co., Ida., U.S.A., August 31st, 1926. Also collected by H. G. Lachmund, on *A. grandis*, Clarkia, Ida., December, 1926; by Boyce, on *A. grandis*, Santa, Shoshone Co., Ida., June 25th, 1927; by C. R. Stillinger, on *A. grandis*, Libby, Mont., August 26th, 1927; by Stillinger, on *A. grandis*, Hougan, Mont., August 31st, 1927; by Lachmund, on *A. grandis*, Cœur d'Alene, Kootenai Co., Ida., September 9th, 1927.

* These measurements were very close to those made by Dr Boyce, extreme range (50) 9·6–13·7 × 5·8–8·9 μ (av. 11·5 × 6·7 μ).

Phomopsis Boycei n. sp.

Pycnidiis discretis vel aggregatis; ab initio subepidermicis denique erumpentibus, carbonaceis, lenticularibus, conoideis, truncatis, vel subglobosis, basibus complanatis, ostiolis paulo pertusis, vel deficientibus, contextu heterogeneo praeditis, matricibus fuligineis supra cavitates sporiferas incrassatulis; pycnidiis parvis, majoribus multilocularibus vel per dissepimentum disruptionem unilocularibus, ceteris unilocularibus, 0·1–0·5 × 0·1–0·4 mm. Sporulis, hyalinis, continuis, guttulatis, inaequalibus, fusoideo-tritraedricis vel fusoideo-tetraedricis, acutis, rarius ellipticis, (100) 9–13 × 4–7·8μ, vulgo 9·9–12·4 × 5–6·8μ; basidiis continuis, subulatis, brevibus, tenuibus, 5–9·9 × 1–2·5μ.

Hab. In ramis emortuis *Abietis grandis* Lindl. in America boreali (Idaho et Montana), August, 1926.

Cultural life-histories of conifer Phomopses.

The perfect stage has been demonstrated for only one of the eight conifer species of *Phomopsis* investigated. In a subsequent paper *Diaporthe conorum* (Desm.) Niessl, will be shown to be the perfect stage of *Phomopsis occulta* Trav. The fact that the ascogenous form could be obtained from monopycnidiospore isolation cultures from pycnospores produced by monoascospore cultures has also been demonstrated. It was the general experience that *P. occulta* was readily produced in culture by monoascospore isolation strains of the fungus.

Throughout the study of the imperfect stage *Phomopsis occulta*, eighty-three forms of this species, representing a wide host and geographical range, have been under observation. In only five (two from inner bark tissue, three from spore horn plantings) has the perfect stage been discovered amongst these, although the forms have been grown on media both natural and artificial, which are known to favour the production of the perfect stage, *D. conorum*. The imperfect stage seems to be thoroughly capable of continually propagating itself, without the formation of the ascomycetous stage. As a general rule, forms of *P. occulta* isolated from pycnidiospores continued to produce the imperfect stage vigorously in culture.

Attempts were made to induce the formation of an ascomycetous stage by growing ninety-four other *Phomopsis* forms on twigs of *Pseudotsuga Douglasii, Chamaecyparis Lawsoniana, Thuja plicata, Abies pectinata, Acer, Ulmus* and *Alnus*; the cultures were kept at approximately freezing temperature for three months, and then brought back to room temperature and placed under moist conditions. The perfect stage was observed in only the few instances cited above.

Diaporthe conorum (41) is reported by Saccardo to be the perfect stage of *Phomopsis conorum*; *D. pitya* (62) the perfect stage of *P. Pseudotsugae*; and the perfect stage of *P. abietina* has been variously reported. Hartig (23) attempted to connect the last fungus with *Peziza calycina* Schum., but his experiments failed. Rehm (36) gave *Dasyscypha calyciformis* (Willd.) Rehm as the perfect stage, but Schellenberg (44) maintained the fungus belonged to another Discomycete. The French mycologists, including Prillieux, Delacroix and Henry, were not able to discover the ascigerous stage, which is still unknown.

In nature *Diaporthe conorum* was observed growing along with *Phomopsis conorum* on the same stem of Sitka spruce. Monoascospore isolations of the *D. conorum* produced only the imperfect stage *P. occulta* in culture. From this experiment it is very evident that *P. conorum* does not belong to the life-history of this *Diaporthe*.

When Wilson (62) reported the perfect stage of *Phomopsis Pseudotsugae* to be *Diaporthe pitya* Sacc., he stated that he sowed ascospores on Douglas fir decoction agar which produced a mycelium similar in appearance to *P. Pseudotsugae*, and in about three weeks' time pycnidia were produced containing the spores of this imperfect fungus borne on long sporophores. I have not been able to repeat Wilson's results, for forms of *Diaporthe conorum* (= *D. pitya*) isolated repeatedly in monoascospore culture produced only the spores of the imperfect stage *P. occulta*. Douglas fir decoction agar was not tested in these experiments, but inoculated twigs of Douglas fir produced *P. occulta* abundantly. *P. Pseudotsugae* did not appear in the cultures of any of the forms of *D. conorum* studied.

Experiments to obtain the perfect stage with forms of *Phomopsis Pseudotsugae* gave negative results. Only the imperfect stage was obtained in experiments which included:

(1) Growth of *P. Pseudotsugae* on natural media (twigs) kept at freezing temperature for three months and then brought back to room temperature where they were kept under moist conditions.

(2) Mixture of twenty-six culture forms of *P. Pseudotsugae*, obtained from single and polyspore isolations, from different geographical sources (Great Britain and the Continent), in eighteen oat agar tubes, two strains in each tube.

(3) Addition of the fungus ferment, Taka-diastase, 0·5 c.c. of 1 per cent., 2 per cent., 4 per cent., 6 per cent., respectively to monopycnidiospore cultures (form No. 43918) on oat agar, after vegetative growth was well advanced.

Culture growth characteristics on sugar-corn meal agar.

Phomopsis occulta. Growth was fairly rapid, appressed, silky, colourless, soon covered by a cottony aerial portion which was indistinctly zonate; the aerial hyphae gradually became coarsely matted, mottled greyish and whitish. Below in the mid- and sub-strata dull olive-green colour* developed. Fruiting was usually abundant. Along the pellicle meandering dark lines were observed, delimiting hyphal areas. Otter-brown colour may or may not appear, tinging the aerial hyphae.

P. juniperovora. Previously reported (17) on corn-meal agar. The typical flaming orange crystals and orange-rufous colour also formed on sugar-corn meal, oat and Leonian's agars.

P. conorum. Growth was fairly rapid, silky, appressed; aerial hyphae arose at the advancing edge of the colony, which became distinctively irregularly zonate as the colony aged. This zonation was observed both in the dark and in light. The aerial growth was whitish, short, dense, somewhat powdery, and in the mid-stratum a dull olivaceous colour appeared, which rapidly darkened. Large, irregular, scattered stromata formed at the base of the tube, which contained occasional spore-bearing locules. Patches of russet-green colour occasionally appeared amongst the aerial growth.

P. montanensis. Growth was slow, strongly appressed, colourless. Within a week, flocculent short, aerial hyphae developed about the inoculum, in the neighbourhood of which an olive-green colour appeared in the mid-stratum, along with abundant fruit bodies. (This green colour was of the same intensity as that formed by *P. Pseudotsugae*.) By the end of two weeks abundant pycnidia studded the surface of the colony for a radius of 10 mm. The colony eventually staled, the hyphae at the periphery becoming old, olive-brown and growing down into the substratum, which was tinged dark brownish; the aerial growth became feltlike and greyish.

P. Strobi. The culture growth characteristics tentatively given were those obtained by culture studies of the *Phomopsis* form isolated by Professor Petri from *Abies pectinata* in Italy. The culture characteristics were distinct from *P. Pseudotsugae*. They were also unlike those of *P. abietina* on the same host.

Growth was rapid, appressed, colourless and silky. A brownish colour appeared in the mid-stratum, staining the medium; this colour continued to keep pace with, but to form just behind the advancing edge of the colony. The aerial stratum had a fine,

* The Répertoire de Couleurs, published (1905) by the French Society of Chrysanthemum Growers, has been consulted for the colour determinations.

granular appearance, indistinctly regularly zonate. Within two weeks the surface over the centre of the colony was covered with abundant pycnidia, which were oozing spores abundantly by the third week. During this period the brown colour in the mid-stratum and throughout the medium had darkened considerably, becoming dull olivaceous. The fine granular character of the aerial hyphae which became greyish was persistent.

P. Pseudotsugae. Growth was fairly rapid, at first colourless, appressed, silky. Within a week a green colour (olive-green) developed in the mid-stratum about the inoculum, and extended practically out to the edge of the colony. The aerial growth was at first short, fibrous, irregular and whitish; this fibrous growth gradually became greyish and irregularly matted. Fruiting was abundant. With age the green colour which had developed in the mid- and sub-strata became dull olive-brown, darkening gradually.

P. abietina. Growth was exceedingly slow. The aerial hyphae were short, dense, felt-like, greyish, overlying a mid-stratum in which a greenish colour developed about the inoculum; later the colour became decidedly brownish (old olive-brown), tinging the aerial hyphae first at the periphery of the colony, which had staled pronouncedly, and then throughout the entire aerial growth. The colony after a month's growth attained a diameter of 4–6 mm. Strands of hyphae were observed to grow deep into the medium. These became dark brownish as did also the medium itself. Fertile pycnidia were not obtained on this medium, or on Leonian's agar. Staling did not occur on oat agar, on which medium fertile pycnidia were obtained.

P. Boycei. Growth was slow, appressed, colourless. The aerial growth was whitish, minutely granular, becoming coarsely granular, overlying a mid-stratum in which a trace of dull olivaceous colour developed. Within two to three weeks yellowish crystals developed in the medium, and tinges of sulphur-yellow appeared in the now greyish aerial stratum. The spores in culture formed slowly, not appearing until fifty days after the culture had been made.

Presence of physiological forms within the species.

During the cultural study, evidence was obtained of the presence of physiological strains within the species. The constancy of the culture growth characteristics for the group has been commented upon. This fact is indeed interesting when one takes into consideration the wide host relationships of certain of the species investigated, *e.g.* general cultural agreement was observed for forms of *P. occulta* isolated from eleven genera, namely, *Taxus, Taxodium, Sequoia, Pseudotsuga, Larix, Picea,*

Abies, Pinus, Juniperus, Thuja, Thujopsis. Slight differences were, however, noted amongst the strains in the amount of pycnidial production, the type of spores produced, the intensity of colour development and the amount of aerial hyphae produced. Certain strains of *P. occulta* were found to be slightly parasitic under conditions of artificial inoculation in the United States ((18) p. 905); other strains of the same species which will be reported later gave negative results when inoculated in Great Britain. Differences such as these when rigorously investigated to determine their stability may prove the presence of physiological strains within the species.

Spore size variation in the conifer *Phomopsis* groups.

Evidence was obtained that a marked constancy with regard to spore size of the *A* and the *B* spores existed in the species investigated, both in nature and in culture. A certain amount of variation in size occurred, but seemingly within a specific size range which could be determined for each group of forms belonging to the given species. It was found that this size range representative of the species could be estimated best by a measurement study of the various host forms which were in agreement with regard to culture growth characteristics. This correlation of morphological with cultural growth evidence clearly indicated that where variation in size occurred this variation was associated with the same physiological forms. It is here interesting to note that Shear, Stevens and Wilcox (47) reported both species, *Botrysphaeria Ribis* Grossenb. & Wigg. and *Physalospora malorum* (Berk.) Shear, as showing remarkable uniformity in the size of their ascospores throughout their host range, whether produced in culture or on the host. Cultural growth characteristics of forms from different hosts were uniform for each species. On the other hand they did not report the same uniformity of size of pycnidiospores of the above species from different hosts. They further stated that as yet they had no satisfactory information as to the extent to which the size of the pycnidiospores could be modified by the environment. Stevens and Jenkins (49), however, had stated that pycnidiospores and ascospores of *Botrysphaeria Ribis* were in satisfactory agreement with regard to size, despite the fact that they came from widely separated hosts (*Rosa, Aesculus* and *Ribes*).

Sherbakoff (48) in his monographic treatment of the genus *Fusarium* on potatoes stated that the most important character in the classification of this group was the type and shape of the conidia, which were sufficiently stable to be used safely in a morphological treatment of this difficult group. Even the size

of conidia, he found, showed a surprising uniformity and stability, when conidia *of the same type* were compared. Wehmeyer (56) regarded spore size as being chiefly valuable as a specific character in *Diaporthe*.

There has been considerable controversy concerning the constancy of spore size and the influence of the substratum upon it. That the size of the individual spore is not fixed was brought out in an interesting experimental study by Hanna (20) who attempted to produce large and small spored strains in pure lines of *Coprinus sterquilinus* Fr. by the continuous selection of large and small spores. He was unable to find satisfactory evidence of the inheritance of individual variations in spore size. He suggested that inasmuch as the mean size of the spores of different fruit bodies of one and the same species of Hymenomycete varies considerably, the spore size given in systematic works ought to be based on measurements of the spores of a number of fruit bodies obtained in different places.

Investigators of the genera *Diaporthe* and *Phomopsis* ((21), (55) p. 393, (65)) have reported general agreement between the sizes of ascospores and pycnospores produced in nature and in culture. The conception of variation in size of spores of *Phomopsis* within a specific range, deduced as a result of the study of spore size amongst conifer species, has been emphasised by Wehmeyer ((55) p. 377) for species investigated within the genus *Diaporthe*.

Spore size variation of the *A* type in *Phomopsis occulta*.

In nature.

The *A* spores of *Phomopsis occulta* were studied in ten forms widely collected from the United States, Canada, Great Britain and Denmark. The average length and width, and the common and extreme size ranges were then determined from the measurement of three hundred and twenty spores. These measurements were used for comparison with those of spores obtained from thirteen other conifer host genera (see Table VI).

A study of the culture growth characteristics of forms isolated from these thirteen hosts with the exception of forms collected on *Abies Veitchii*, *Tsuga canadensis* and *Cryptomeria japonica* which were not studied in culture, showed resemblance amongst themselves and with the forms of the species *Phomopsis occulta* on Douglas fir. It was therefore natural to expect that the size range obtained from a study of these different host forms would closely overlap the range of species on Douglas fir, and that if variation occurred, it would be within the range determined for the forms on Douglas fir, provided of course these measurements

were truly representative of the organism throughout its range of size variation.

Table VI. *Averages and extreme ranges of* A *spores of* P. occulta *on Douglas fir and other hosts compared.*

Host	No. of spores	Average Length × Width (μ)	Extreme range Length × Width (μ)
Pseudotsuga Douglasii ...	320	7·4 × 2·4	5·3–12·4 × 1·6–3·1
Abies pectinata	50	7·9 × 2·4	6·2–12·4 × 1·9–3·1
*A. homolepis**	10	7·7 × 2·4	6·8–10·5 × 1·9–2·5
*A. Veitchii**...	10	7·2 × 2·2	5·3–8·1 × 1·9–2·5
Picea excelsa	10	7·8 × 2·1	5·6–9·0 × 1·9–2·5
Larix europaea	80	7·5 × 2·4	5·6–10·2 × 1·9–3·1
*Tsuga canadensis**	10	7·8 × 2·5	6·2–9·9 × 1·9–3·1
*Taxus baccata**	10	7·9 × 2·4	6·2–9·3 × 2·2–2·8
T. baccata fastigiata ...	20	7·5 × 2·4	5·9–11·2 × 1·9–3·1
*T. cuspidata**	10	7·6 × 2·3	6·2–9·3 × 1·6–2·8
*Sequoia sempervirens** ...	40	7·7 × 2·3	6·2–10·2 × 1·9–3·1
*S. gigantea**...	10	5·6 × 2·0	5·0–6·8 × 1·6–2·2
*Taxodium distichum** ...	10	7·4 × 2·4	5·6–8·1 × 2·2–2·8
*Cryptomeria japonica** ...	10	7·1 × 2·8	5·6–8·7 × 2·2–3·1
Pinus sylvestris	10	7·6 × 2·3	6·5–8·1 × 2·2–2·5
*Juniperus virginiana** ...	20	7·6 × 2·5	6·5–8·7 × 2·2–2·8
*Cupressus sempervirens** ...	10	7·9 × 2·4	6·9–8·7 × 2·2–2·5
Thuja plicata	50	7·2 × 2·2	5·3–8·7 × 1·6–2·8
*Thujopsis dolobrata** ...	10	6·6 × 2·6	5·6–7·1 × 2·2–3·1
Total—13 host genera ...	380	7·5 × 2·4	5·0–12·4 × 1·6–3·1

* Forms collected in the United States; forms on *Larix* and *Pseudotsuga* collected on both sides of the Atlantic have been grouped for convenience.

In Table VI it will be observed that while variation in spore size of the species on the thirteen host forms occurred, this variation was within the actual range determined by the measurements of spores of the Douglas fir forms collected on both sides of the Atlantic. Where variation was most marked in the forms collected on *Sequoia gigantea* and *Thujopsis dolobrata*, only a scant number of abnormally small *A* spores were observed along with a great abundance of *B* spores.

In culture.

The Douglas fir forms which had been studied in nature were found to produce spores under conditions of artificial culture which agreed in size with those formed naturally. Variation occurred, but within the specific range determined for the species. The close agreement between naturally and culturally produced spores is shown in Table VII. A variety of artificial substrata are indicated which apparently had very little or no effect in influencing the size of the spores. It will be noted that on elm twigs the spores tended to be somewhat shorter, although this host substratum had shown itself to be a very congenial

one for the growth of *Diaporthe conorum* (*Phomopsis occulta*), hence the diminution in length should very probably be interpreted in terms of inherent variation incident upon growth conditions of the fungus rather than any direct influence of the host itself. There would appear to be a tendency shown by the organism to produce in culture a fewer number of the longer spores occurring in the upper limits of the size range.

Table VII. *Averages and ranges of spores of* P. occulta *produced on artificial hard agars and natural media compared.*

Substratum	No. of spores	Average Length × width (μ)	Average range Length × width (μ)	Extreme range Length × width (μ)
Pseudotsuga Douglasii (Nat.)	320	7·4 × 2·4	6·4–7·9 × 2·1–2·6	5·3–12·4 × 1·6–3·1
Sugar-corn meal agar	160	7·2 × 2·3	6·8–7·5 × 2·0–2·5	5·6–9·3 × 1·6–3·1
Oat agar	80	7·1 × 2·3	6·9–7·2 × 2·3–2·5	5·6–9·0 × 1·6–2·8
Leonian's agar	70	7·1 × 2·4	7·0–7·3 × 2·3–2·5	5·0–8·7 × 1·9–3·1
P. Douglasii twig	90	7·5 × 2·3	7·2–7·8 × 2·2–2·5	6·2–9·3 × 1·6–2·8
Acer Pseudoplatanus twig	40	7·4 × 2·5	6·9–7·9 × 2·4–2·6	6·2–9·3 × 1·9–3·1
Ulmus campestris twig	30	6·7 × 2·3	6·1–7·0 × 2·2–2·3	5·9–8·1 × 1·6–3·1
Alnus sitchensis twig	10	7·3 × 2·3		6·2–9·3 × 1·9–2·5
Total average (45 cultures)	480	7·2 × 2·4	6·1–7·9 × 2·0–2·6	5·0–9·3 × 1·6–3·1

In order to test further any possible influence the artificial substratum might have in affecting spore size, measurements were made of spores of forms representing seven generic hosts, produced on both hard agars and natural media (the same media used for the Douglas fir forms presented in Table VII). These comparisons between naturally and culturally produced spores

Table VIII. *Averages and ranges of spores of* P. occulta *produced in nature and culture compared.*

Generic host	Nature or culture	No. of spores	Average Length × width (μ)	Extreme range Length × width (μ)
Abies (2 species)	Nat.	70	7·8 × 2·4	5·3–12·4 × 1·9–3·1
	Cult. (9)	140	7·3 × 2·3	5·9–9·6 × 1·6–2·8
Larix europaea	Nat.	80	7·5 × 2·4	5·6–10·2 × 1·9–3·1
	Cult. (5)	50	7·5 × 2·4	5·3–9·0 × 1·9–3·1
Taxus (3 species)	Nat.	40	7·6 × 2·4	5·9–11·2 × 1·6–3·1
	Cult. (9)	90	7·4 × 2·2	6·2–9·3 × 1·6–3·1
Sequoia sempervirens	Nat.	40	7·8 × 2·3	6·2–10·2 × 1·9–3·1
	Cult. (3)	30	7·9 × 2·3	5·6–10·2 × 1·9–3·1
Thujopsis dolobrata	Nat.	10	6·6 × 2·6	5·6–7·1 × 2·2–3·1
	Cult. (7)	70	7·6 × 2·3	5·9–9·9 × 1·9–3·1
Juniperus virginiana	Nat.	20	7·6 × 2·5	6·5–8·7 × 2·2–2·8
	Cult. (1)	10	7·8 × 2·5	7·1–8·4 × 2·2–2·8
Thuja plicata	Nat.	50	7·1 × 2·2	5·3–8·7 × 1·6–2·8
	Cult. (4)	40	7·1 × 2·3	5·9–8·7 × 1·9–3·1

are presented in Table VIII. The substratum apparently did not affect spore size. Slight variation occurred, but within the given specific range. It is here extremely interesting to note that spores of the *Thujopsis* form which were exceedingly small in nature regained a normal size under culture conditions.

The spore size of *Phomopsis conorum*.

In nature.

A measurement study of two hundred and eighty fusoid spores of *Phomopsis conorum*, representing thirteen forms of the species widely collected on *Pseudotsuga Douglasii* in Great Britain and in Holland and Denmark, showed a spore range which at first appeared to be specific; for when *A* spores of forms of apparently the same species were studied with regard to this morphological character on another host, *Picea*, variation in size was noted, but this variation was within the range determined for spores of the Douglas fir forms. The extreme range of the length and width of the two hundred and eighty spores measured from Douglas fir was 6·2–13·6 × 2·5–4μ (av. 9·5 × 3·1μ); the extreme range of one hundred and twenty spores of these forms studied on branches of *Picea sitchensis* and cones of *P. excelsa* was 6·2–13 × 2·5–4μ (av. 10·1 × 3μ).

Another form of *Phomopsis conorum* was discovered on *Pinus Strobus* which appeared to be the same species but on a new generic host. This form produced larger spores (twenty spores, extreme range, 9·9–14·6 × 2·8–4·7μ, av. 12·2 × 3·4μ) which were typical in shape. The inclusion of the white-pine form, therefore, would tend to extend the spore range of the species. At first it was thought that the Weymouth pine strain might be possibly distinct physiologically, and to determine this point the fungus was isolated in pure culture. The culture growth characteristics of the strain were, however, identical with those of the Douglas fir and spruce forms on the same media. The fact that the *P. Strobus* form potentially was able to produce smaller *A* spores under artificial conditions, will be brought out in the next section in the discussion of spores of *P. conorum* produced in culture. A consideration of the foregoing data emphasises the importance of a complete knowledge of a given fungus species, with regard to the extent of variation of spore size throughout the entire host range of the organism.

In culture.

Phomopsis conorum did not produce *A* spores vigorously in culture as did *P. occulta*. Only four of the eight forms of *P. conorum*, isolated for life-history study, reproduced spores.

On natural media where one would ordinarily expect abundant fructifications producing the fusoid type, pycnidial stromata formed but, in these, spores were produced slowly. Throughout the culture examination, *B* spores generally were found associated with a scant number of the *A* type, which formed later. In such cases the *A* spores were inclined to be much shorter and were produced at the lower part of the spore range determined for naturally produced spores. It was observed that in the one case where an abundance of *A* spores formed in culture on sugar-corn meal agar, the spores were larger than the fusoid type which occurred likewise in culture on oat agar, amongst a preponderance of the *B* type. These artificially produced *A* spores were practically identical in average size and actual range with naturally formed spores of the same fungus strain on the Douglas fir.

In the Weymouth pine form, the culture-produced spores which formed slowly, associated with abundant *B* spores on an artificially inoculated elm twig, were considerably shorter than those found in nature. The average spore size (av. twenty spores, 9·3 × 3·2μ) and extreme range (7·8–11·2 × 2·8–3·7μ) overlapped closely the range of naturally produced spores of forms on Douglas fir, but, even in this instance, spore size under artificial conditions, especially with regard to length, appeared to be slightly smaller. As in *Phomopsis occulta*, *P. conorum* in culture did not produce spores at the upper limits of the size range of naturally produced spores.

The *A* spore size in *Phomopsis juniperovora*.

In nature.

A measurement study of a hundred *A* spores of *Phomopsis juniperovora* representing nine forms collected from widely distributed sources in the United States on *Juniperus virginiana* showed a series of averages which were in exceedingly close agreement with each other. Variation in size occurred, but this variation was within a more or less prescribed range, extreme range 5·6–11·5 × 1·9–3·1μ (av. 8·5 × 2·4μ). Measurements of thirty spores of three strains of the species on *Cupressus* gave an average (8·4 × 2·4μ) which was practically identical with that from *Juniperus*; the actual range of spores on *Cupressus* (6·8–9·9 × 1·9–2·8μ) was within that determined for the fungus on Juniper.

In culture.

It was observed that certain of the forms of *Phomopsis juniperovora* which had been in culture for an extended period of time lost their ability to produce fertile fruit bodies. Pycnidia

were not observed to form abundantly when the forms were freshly isolated. Forms Nos. 41041, 41048 and 41376, isolated from *Juniperus virginiana*, *Cupressus arizonica* and *Chamaecyparis obtusa*, respectively, continued to produce spores sparingly although they had been maintained under artificial conditions in culture for four years. The reduced number of spores which formed under artificial conditions were normal, agreeing closely in size with those produced by a recently isolated form, No. 43968, obtained from diseased material of *Juniperus virginiana*.

A measurement study was made of a hundred spores (av. 8·3 × 2·4μ) produced under artificial conditions by the three forms on oat and sugar-corn meal agars, and on natural media—twigs of Douglas fir, elm, sycamore and alder. The average range closely overlapped that of naturally produced spores; the extreme range was 6·2–10·2 × 1·9–3·1μ. The tendency exhibited by other *Phomopsis* species to produce a reduced number of the long spores in culture was shown in a like manner by forms of *P. juniperovora*.

The *A* spore size variation in *Phomopsis montanensis*, *P. Pseudotsugae*, *P. abietina* and *P. Boycei*.

Variation in *A* spore size, but within a more or less prescribed range, was observed amongst spores produced in nature and culture by the species *Phomopsis montanensis*, *P. Pseudotsugae*, *P. abietina* and *P. Boycei*.

The extreme range of a hundred spores measured of the type specimen of *P. montanensis* was 5·3–9·3 × 2·2–3·4μ (av. 6·9 × 2·8μ); the extreme range of fifty spores produced on Leonian's agar was 5·6–8·1 × 2·2–3·4μ (av. 6·8 × 2·7μ).

The actual range of two hundred and ten spores of ten forms of *Phomopsis Pseudotsugae* collected on Douglas fir and on larch in Scotland and in Denmark, Sweden and Holland was 4·7–12·4 × 1·9–3·4μ (av. 6·7 × 2·6μ). These forms showed a constant cultural agreement. Wilson (62) had given the range as 5·5–8·5 × 2·5–4μ and stated the size to be fairly constant, showing little variability. I, however, found that three of the forms measured showed greater amount of variation, producing spores which were longer than those of the remaining seven forms investigated. The inclusion therefore of these would extend the range above the figure for length reported by Wilson. In culture fifty spores of four forms gave an actual range of 5–7·4 × 2·2–3·4μ (av. 6·2 × 2·8μ), these figures indicating very little variation with regard to length and width; the extreme range was within that given by Wilson. It is here interesting to note that only one long spore was observed among the culturally produced spores measured; this spore had a length of 9·3μ.

In the above two instances, the spores of *Phomopsis montanensis* and *P. Pseudotsugae* produced in culture, while normal in size, did not include the longer spores which appeared in nature at the upper part of the actual range. When, however, spores of *P. abietina* produced in culture and in nature were compared, the opposite apparently held, for spores produced in culture extended the length range. A measurement of seventy spores from fresh material collected in the Jura, France, gave an actual range of 8·4–14·9 × 3·7–5·6μ (av. 12·4 × 4·6μ). This range included those determined for three collections in the herbaria of Magnus, Tubeuf and Hartig, respectively, and would therefore appear to be specific. Measurements of sixty spores of the Jura form (No. 43966), produced in culture on oat agar and natural media, however, gave an actual range, 10·2–16·4 × 3·7–5·6μ (av. 13·5 × 4·5μ). This overlapping of the ranges of naturally and artificially produced spores and the extension of the length range by the latter is also interpreted as being due to the inherent variability of the species under certain growth conditions rather than to any direct influence of the host substrata. Further investigation of the size of spores exhibited by a number of forms collected from various sources on *Abies pectinata* on the Continent will very probably demonstrate that spores longer than those measured from specimen No. 43966 will be found.

Spores of *Phomopsis Boycei* produced in culture likewise slightly extended the upper range for length. Measurements of a hundred spores of the type specimen gave an actual range of 9–13 × 4–7·8μ (av. 11·1 × 5·9μ); fifty measurements of a form of the same species made by Dr Boyce, who submitted the same to the author, showed an actual range of 9·6–13·7 × 5·8–8·9μ (av. 11·5 × 6·7μ). In culture, form No. 43977 produced on oat agar and natural media spores with an extreme range of 9·3–14 × 3·7–7·5μ (fifty spores, av. 11·2 × 5·6μ). The foregoing measurements demonstrate the close overlapping which exists between the range of naturally and culturally produced spores. Among the latter it was observed that those produced on oat agar tended to be somewhat narrower than those produced on twigs of *Abies*, *Pseudotsuga*, *Ulmus* and *Acer*.

The *B* spore size variation in *Phomopsis* species.

It was found very difficult to measure the *B* type spores accurately because of their curvature and their crooked ends, hence the measurements obtained only approximated to the actual length of the spores. Wherever possible in measuring *B* spores, spores were selected which were inclined to be straight. Spore width, which is approximately 1μ, was not considered. Despite the difficulty in measuring the *B* spores, it was found

that the measurements of a considerable number of the filamentous bodies produced in culture on hard agars and natural media agreed surprisingly in size with the spores produced in nature. Wilson (64) has found that agreement between the sizes of *B* spores of *Myxosporium* produced in nature and culture also held true.

Measurements of one hundred and sixty-two spores produced in nature by forms of the species *Phomopsis occulta* gave an actual length range of 15·2–34·4μ, average length range 20·9–27μ (av. 23·1μ). A measurement study of four hundred and forty-two spores produced in forty-four cultures showed the extreme range to be 10·2–34·1μ, average range 20·9–26·7μ (av. 22·7μ).

Spores of *Phomopsis conorum* produced in culture showed a satisfactory agreement with naturally produced *B* spores. As in the *A* spores a certain amount of variation occurred. In this connection it was observed that the *B* spores tended to be slightly longer when produced in great abundance along with only a scant number of *A* spores. In nature, one hundred and fifty-four spores of forms of the species *P. conorum* showed an extreme length range of 15·5–34·4μ, average length range 20·2–24·3μ (av. 22·2μ). In culture forms of the same species, eighty spores had an actual range of 17·7–34·1μ, average range 22·2–26·9μ (av. 24·2μ). Despite the unsatisfactory manner of measuring these filamentous spore bodies, it must be admitted that the tendency for the size ranges of the two lots of spores compared to overlap is very pronounced.

In nature the *B* spores of *Phomopsis juniperovora*, as in the species *P. occulta* and *P. conorum*, were observed occurring commonly. The ratio of *A* spores to *B* spores was, however, extremely variable. Culturally only a reduced number of spores were produced by *P. juniperovora*. The *B* type spores were found occurring only scantily amongst the *A* type, and only a very few were obtained for measurement. The actual length range of these agreed closely with that of *B* spores produced in nature.

Intermediate spore size variation.

A limited number of measurements were made of the intermediate spores of *Phomopsis occulta*. These variously shaped attenuated spores intergrading between the *A* and *B* types also evidenced a certain constancy with regard to size, and while variation occurred it took place apparently within a limited range as it did in the *A* and *B* spores. A measurement of eighty intermediate spores produced by forms of the species representing six generic hosts showed an actual range of 8·7–15·5 × 1·2–2·5μ, average range 10–14·3 × 1·2–2μ (av. 10·9 × 1·7μ). Forms of the same species in culture (eighty spores) showed an

extreme range, 8·4–17·7 × 0·9–2·5μ, average range 10·9–14 × 1·2–2μ (av. 12·2 × 1·5μ).

Intermediate spores were not produced nearly so abundantly in nature by *Phomopsis conorum* as they were by *P. occulta*. A measurement study of fifty spores found in seven collections of the species indicated an actual range of 11·8–17·4 × 1·2–2·5μ. A scant number of intermediate spores were observed in only one culture, which produced mostly *A* spores. The range of these spores was found to be within that of intermediate spores produced in nature.

Variation in spore shape of *Phomopsis* sp. in nature and culture.

The pycnidiospores, both *A* and *B*, of the coniferous *Phomopsis* species, showed for the most part a marked agreement in spore shape, not only throughout their respective host ranges, but also amongst spores produced artificially on a wide variety of synthetic and natural media (twigs of both coniferous and broad-leaved hosts), provided that the same type of spore was considered in making the comparison. This stability of spore shape was particularly striking in *Phomopsis occulta*, which is widely distributed geographically, and which has a considerable host range. A very close relation between this species on conifers and forms on broad-leaved hosts is strongly indicated.

The agreement between the *B* spores of *Phomopsis conorum* produced in nature and culture was most pronounced. When the horseshoe-shaped *B* spores were first observed, it was of considerable interest whether or no this character of curvature would persist in spores produced under artificial conditions. In culture similar curved spores were likewise obtained and this curvature must therefore be considered inherent in the species; as an aid in the identification of the species it will undoubtedly prove a most helpful character.

When Hartig, and Prillieux and Delacroix described *Phoma abietina* and *Fusicoccum abietinum*, respectively, they did not mention the occurrence of irregularly shaped spores with protuberances amongst the typical spindle-shaped type which they reported. Wilson (62), however, in differentiating his fungus *Phomopsis Pseudotsugae* from *Phoma abietina*, commented upon and figured the latter fungus after an examination of the Hartig specimen at the Royal Botanic Garden, Edinburgh; he recorded an irregularity in form of the fusoid type. I have examined the same specimen but unfortunately it contained only a very scant number of spores which were considerably desiccated. Those that were observed were decidedly irregular in shape. Further examination of other exsiccata and living material freshly

collected showed that the regular spindle-shaped spores predominated, but that irregular spores with protuberances were present. In culture the spindle-shaped spore likewise predominated but irregular spores occurred. On the other hand *P. Boycei* produced an abundance of irregular spores, which were much distorted, in culture; as in nature only a very few regular fusoid spores were to be found. In *P. juniperovora* and *P. Pseudotsugae*, however, spores "pinched in" at the median part of the spore bodies, in the former, and typical elliptic-fusoid spores, in the latter, were not so evident amongst culture-produced spores.

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Summary.

An investigation of the present known *Phomopsis* species on conifers has been undertaken for the purpose of differentiating *P. Pseudotsugae* the cause of the *Phomopsis* disease of Douglas fir, from closely allied forms occurring on Douglas fir and other conifer hosts.

The present status of the genus *Phomopsis*, now generally regarded as the imperfect stage of *Diaporthe*, is discussed. Upon the basis of a broad conception of the genus certain atypical forms whose perfect stages are still unknown are included in the *Phomopsis* group. These forms approach the form genus *Fusicoccum* although they appear to have a greater affiliation with

Phomopsis. Until the perfect stages have been discovered these species on the border-line of the genus have been placed provisionally in *Phomopsis*.

Eight species are differentiated—*Phomopsis occulta* Trav. [*Diaporthe conorum* (Desm.) Niessl], *P. juniperovora* Hahn, *P. conorum* (Sacc.) Died., *P. montanensis* n. sp., *P. Strobi* Syd., *P. Pseudotsugae* Wilson, *P. abietina* (Hart.) Wilson & Hahn and *P. Boycei* n. sp. A dichotomous key is given.

Phomopsis occulta which has been culturally proven the imperfect stage of *Diaporthe conorum* is the only species of the conifer group whose complete life-history has been discovered. *P. conorum*, which inhabits cones and other plant parts as well, does not belong to the life-history of *D. conorum*.

The conifer *Phomopsis* spp. exhibited great constancy with regard to culture growth characteristics. The characters on a single medium are described for the group. Variability amongst the morphological characters was observed. The characters of the pycnidial stromata were by no means constant. Spore shape and size on the other hand were fairly constant and could be relied upon as specific characters, providing the same type of spore was considered. Variation in size occurred, but within a specific range, which could be determined by a measurement study of forms throughout the host range of the species. Spores produced in culture on artificial and natural media showed satisfactory agreement with spores produced in nature. There were indications of physiological strains within the groups of forms studied.

The conifer *Phomopsis* spp. showed both wide and extremely limited host relationships. Certain of the species are now known to be widely distributed geographically, occurring on a comparatively large number of hosts, *e.g. P. occulta* occurred on fourteen host genera and its habitat included both North America and Europe, whereas *P. abietina* appeared to be limited to the smaller branches of a single host, and to occur only on the Continent in Germany and France.

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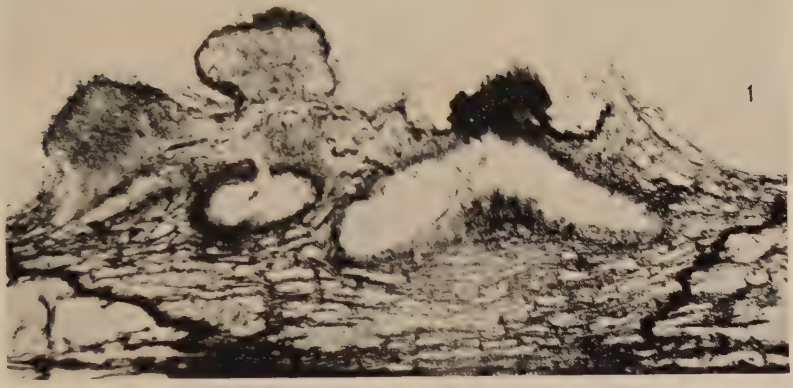
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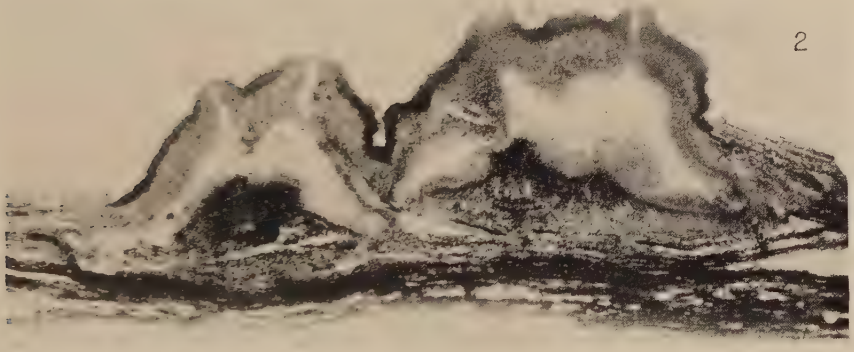
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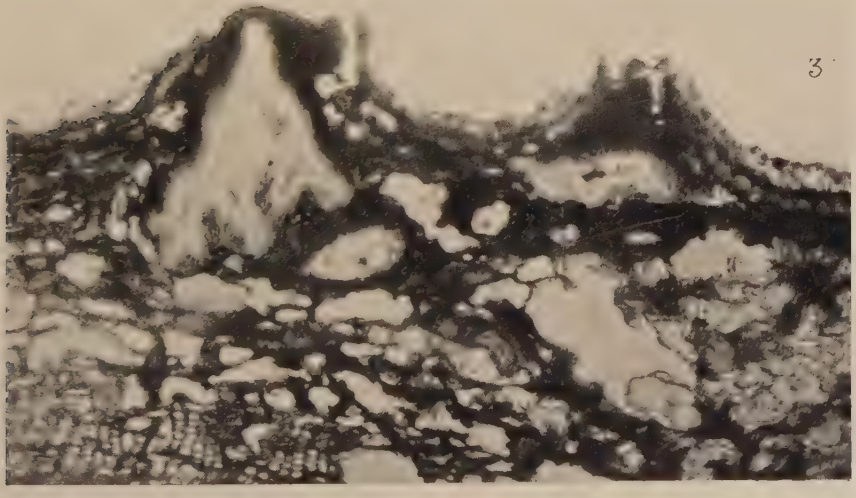
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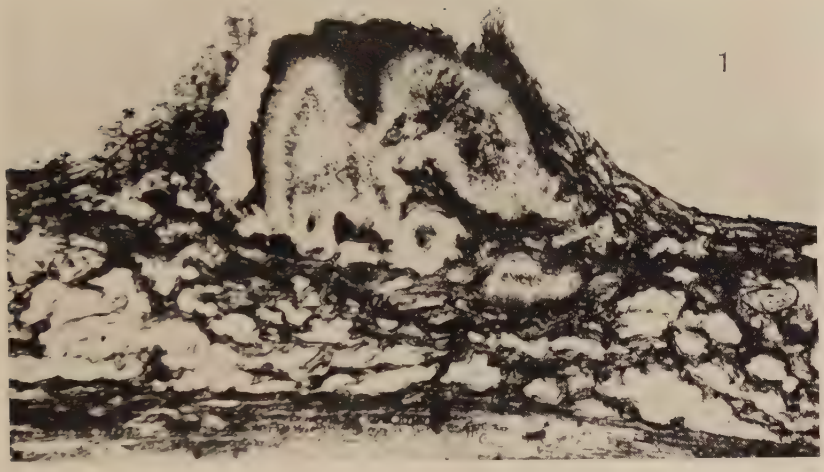
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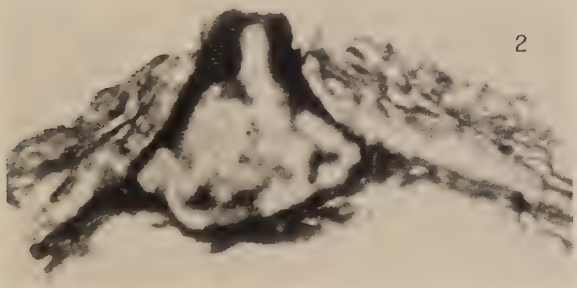
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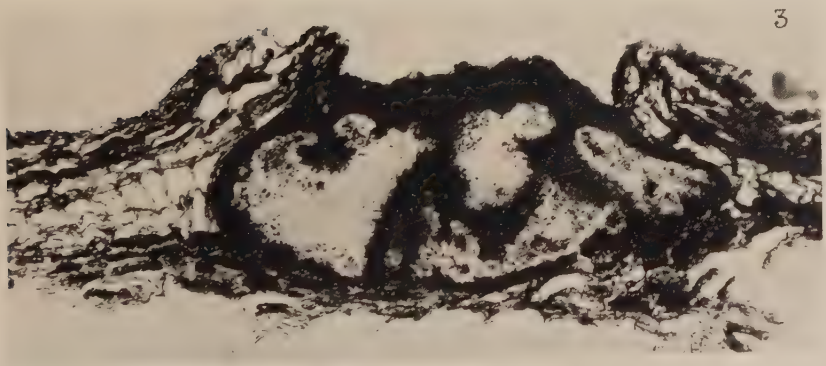
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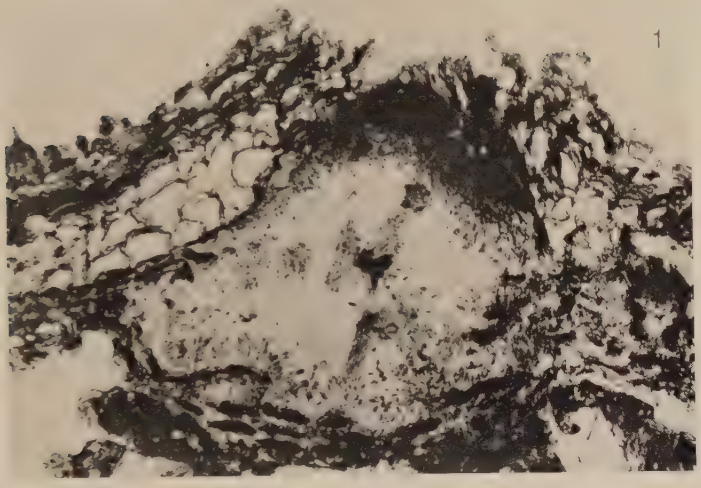
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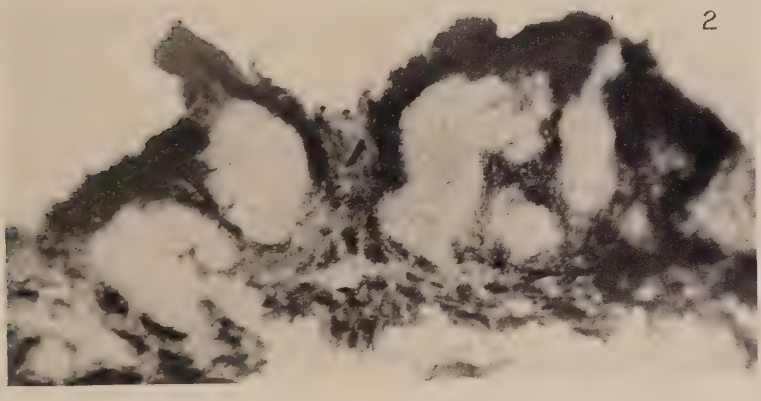
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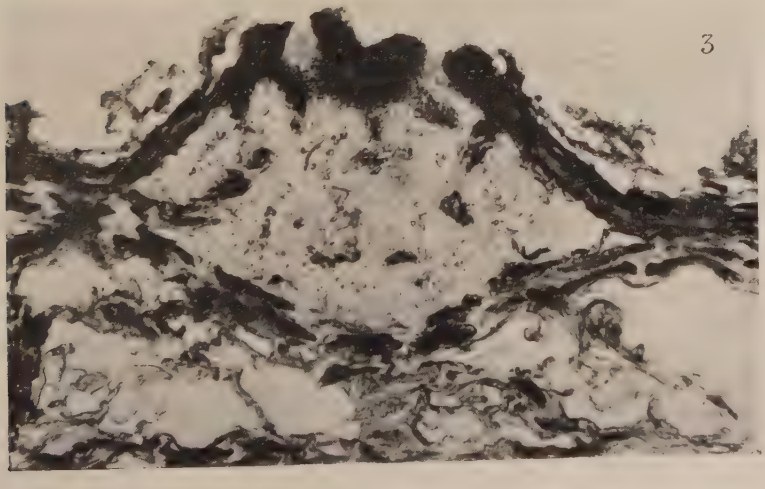
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DESCRIPTION OF PLATES.

PLATE I.

Fig. 1. Pycnidia of *Phomopsis occulta* (*Diaporthe conorum*) in the upper cortex of *Pseudotsuga Douglasii*, associated with a more or less differentiated light-coloured entostromatic area indicated by a blackened zone dipping down into the inner cortex. × 80.

Fig. 2. Compound pycnidia of *P. conorum* on the cone scale of *Picea excelsa*; cavities tending to fuse forming an irregular elongate chamber with protrusions. × 45.

Fig. 3. Simple pycnidia of *P. Pseudotsugae* embedded in the upper cortex of *P. Douglasii*; unilocular cavity formed by the complete fusion of several chambers formed above each other. × 130.

PLATE II.

Fig. 1. Compound pycnidium of *Phomopsis Pseudotsugae*; an isolated pycnidial locule is shown amongst the cells of the cortex. × 130.

Fig. 2. Pycnidium of *P. montanensis* on *Abies lasiocarpa*; the fusion of the chambers is almost complete and a unilocular fruit body has been formed. × 130.

Fig. 3. Compound pycnidium of *P. montanensis*. × 130.

PLATE III.

Fig. 1. Embedded compound pycnidium of *Phomopsis abietina* on *Abies pectinata*, showing the thin walls on the floor and at the sides of the fruiting structure. × 130.

Fig. 2. Simple and compound pycnidia of *P. abietina*. × 130.

Fig. 3. Compound pycnidium of *P. Boycei* on *A. grandis*. × 130

A METHOD FOR THE PRESERVATION OF PETRI DISH CULTURES OF FUNGI.

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The development of technique for the cultivation of fungi has progressed rapidly during recent years, but at present there is no satisfactory method in general use for the preservation of fungus cultures for future reference. Dr Bewley (*Ann. Appl. Biol.* xiii (1926), 577–579) has suggested dissolving off the agar in boiling water and transferring the fungus growth to glass, on which it is dried; but this method does not appear to have been adopted to any appreciable extent. A great deal of the value of cultures is lost because of their evanescent character and the desirability of having permanent records of fungi in culture must be evident to every mycologist. This applies especially to herbaria, where cultures are frequently received for identifica-

tion and where comparative cultural material is for the most part lacking. The establishment of type collections of fungi has relieved the situation, but the liability of fungi to saltate, and the extreme difficulty experienced in maintaining some in a fruiting condition, limit slightly the usefulness of these collections. The following method whereby cultures of fungi can be preserved indefinitely as herbarium specimens has recently given satisfactory results and is described in the hope that it may be of interest to others.

The fungus is grown in Petri dishes on clear maize meal agar prepared as follows: 25 gm. ground maize are added to 500 c.c. water and steamed at a temperature not exceeding 60° C. for an hour, then strained through fine cheese cloth and afterwards through filter paper, and the volume made up to 500 c.c. Difco agar (6 gm.) is then added and the mixture boiled until this is dissolved; the medium is then tubed and sterilised (Sherbakoff's medium—*Phytopath.* VII (1917), 126—slightly modified by Ashby). When required, the medium is poured into Petri dishes of 10 cm. diameter and inoculated in the ordinary way. As soon as the desired stage of development of the fungus is reached the agar is cut round the sides with a scalpel to free it from the glass. One edge of the agar is then carefully lifted by the scalpel and a few drops of water introduced between the underside of the agar and the bottom of the Petri dish. Without allowing the agar to drop the scalpel is replaced by an aluminium lifter and by careful manipulation half the agar at least is loosened from the bottom of the Petri dish, more water being added to facilitate this if necessary. The fingers are then placed under the agar, which is lifted bodily from the dish and laid flat on a piece of polished waxed cardboard (soaked in melted wax of 115° F. M.P. and preferably with a layer of wax $\frac{1}{4}$ inch thick on the surface) on which a large drop of water has been placed. The agar floats out flat on the waxed cardboard and any air bubbles are forced to the edge by the aluminium lifter. The excess water is carefully drained off, and the cardboard with the culture inverted and placed to dry so that no dust can fall on the surface of the culture. A simple framework allowing free access of air to the agar can be used to support the drying cultures. At laboratory temperatures the drying is usually effected in twenty-four hours but may take more than two days if the agar is thick. When quite dry the agar can be peeled off the waxed surface with a knife, and immediately placed first in waxed paper envelopes and then in the herbarium envelope. The surface of the culture is not disturbed during the whole process and portions of the culture can be cut off with scissors and mounted in lactic acid for microscopic examination. There is a tendency

for the wax to adhere to the back of the agar but this interferes little with the microscopic field. Attempts to employ ferrotype plates as used for glazing photographic prints, or cardboard soaked in a hard wax, were not satisfactory as the agar cultures peeled off during drying and were therefore very uneven. Good results were achieved, however, by placing centrally on the waxed cardboard a circular disc cut from a ferrotype plate. The disc should be about 7·5 cm. in diameter and is pressed down on the wax while it is still soft; the superfluous wax is subsequently cleaned away with a ruler to give a wax surface level with the disc. The agar culture in drying is held flat by the wax which it overlaps while the central portion does not come into contact with the wax at all. Portions of agar cultures cut from the central part of a Petri dish (and consequently without the thick rim formed by the agar where it runs up the vertical sides of the dish) sometimes dry satisfactorily on the rigid ferrotype disc even when they do not overlap the wax; for such preparations it is preferable to have a margin of free agar surrounding the fungus colony. It is important to clean the ferrotype disc thoroughly with water and then with a saturated solution of beeswax in petrol to prevent the agar film sticking to it. The best culture medium to use is undoubtedly the one given above but it does not suit all fungi; preparations on Dox, malt extract, Quaker oat, and peptone cane sugar agars have, however, been made successfully. Richards's agar is impracticable as the ingredients render the agar very fragile. It is advisable to choose Petri dishes which are flat, as those raised in the centre thin out the agar film at that region and it is then liable to dry out and adhere to the glass.

Cultures preserved in this way are extremely convenient for sending by post and though, of course, the spores are very apt to become detached from the conidiophores, yet, nevertheless, preparations made from them are valuable for comparative purposes. It may also be mentioned that lantern slides are readily prepared simply by mounting the dried culture between two squares of glass.

ON THE OCCURRENCE OF "FALSE SECTORS" IN CULTURES OF FUSARIUM FRUCTIGENUM FR.

By R. N. Sahai Vasudeva, Ph.D.

(With Plate IV.)

Introductory.

In the course of some laboratory experiments in which the growth rates of a strain of *Fusarium fructigenum* were being tested under different conditions of acidity and alkalinity, one of the plates showed the peculiar appearance illustrated in Pl. IV, fig. 1. The edge of the colony was very irregular owing to the development of five spreading fan-shaped sectors. When isolations were made from these the five resultant cultures proved to be the same and all differed from the parent in showing much greater growth of aerial mycelium with corresponding reduction in the amount of sporulation.

The plate concerned contained glucose peptone agar with 0·08 per cent. malic acid. Incidentally it should be added that this was the only plate in the series in which the layer of medium was poured shallow. The importance of this point will be emphasised later.

The strain of *Fusarium fructigenum* which gave rise to the above appearance was one (strain *A*) which had been studied in detail by Brown(1), who did not describe or figure sectors of the peculiarly spreading type shown in Pl. IV, fig. 1. It was decided, therefore, to investigate the occurrence of such sectors more closely, and in particular to determine whether their appearance could be correlated with the nature and amount of the cultural medium employed.

Experimental.

(1) *Fungi and media used.*

Fusarium fructigenum, strain *A*, was chiefly used in these experiments. Four other strains were also used in a few tests, with results closely similar to those found to apply for strain *A*. The purity, *i.e.* freedom from admixture, of all the stock cultures was guaranteed at the beginning of the work by carrying on each from a single hyphal tip.

The following media were employed:

(1) Glucose peptone agar:

Glucose	10 gm.
Peptone	2 ,,
Potassium di-hydrogen phosphate (KH_2PO_4)	1 ,,
Magnesium sulphate	0·5 ,,
Agar	15 ,,
Distilled water	1000 c.c.

(2) Malt agar:

Malt	20 gm.
Agar	15 ,,
Distilled water	1000 c.c.

(3) Brown's agar:

Glucose	2 gm.
Asparagin	2 ,,
Normal potassium phosphate (K_3PO_4)	1·25 ,,
Magnesium sulphate	0·75 ,,
Agar	15 ,,
Distilled water	1000 c.c.

(2) *Depth of medium as affecting sector formation.*

The effect of this factor is very clearly marked. It is only in shallow plates that sectors of the markedly diverging type occur. This is in agreement with the results described by Christensen (2) for *Helminthosporium sativum.*

Plates of varying thickness of medium were poured: (1) 1 cm. deep, (2) $\frac{1}{2}$ cm. deep, (3) very shallow. In the last, a few c.c. (about 7) of medium were poured while still rather warm into the sterilised plate which was shaken to spread the medium over the whole surface. The degree of shallowness was somewhat variable, partly on account of the fact that the bottoms of the Petri dishes were not all perfectly flat. In order to eliminate errors due to this variability, a large number of Petri dishes (10–15) were poured for each. The results were as follows:

Of ninety-three deep-poured plates, none showed the presence of sectors, whereas of one hundred and forty-eight plates which were poured shallow, ninety-five developed sectors.

Pl. IV, fig. 2, illustrates the appearance of *Fusarium fructigenum* strain *A* on a deep layer of glucose peptone agar. Pl. IV, figs. 3, 4, show the characteristic lobed or sectored appearance of the fungus when grown on a shallow layer of the same medium. Exactly similar results were obtained with cultures of four other strains of *Fusarium fructigenum.*

A simple method of demonstrating the effect of shallowness of the medium on the occurrence of sectors is to pour the plate in such a way that the medium grades from very shallow on one side to deep on the other. When such a plate is inoculated at the centre it is found that diverging sectors appear in a high percentage of the plates but only on the side where the medium is shallow. The non-appearance of sectors in some is in all probability due to the fungal culture becoming stale and ceasing to grow before its margin has reached a sufficiently shallow region of the plate. The position of the inoculum, therefore, to some extent determines whether sectors will arise or not. Pl. IV, figs. 5 and 6, illustrate the phenomenon just described, the shallow side of the medium being upward in each case.

(3) *Composition of medium as affecting sector formation.*

The experiments in this connection were carried out with the glucose peptone medium. Various modifications of this were prepared and used for shallow plate cultures.

On the complete medium as given on p. 97, sectors were freely formed. Omission of the magnesium sulphate constituent had no obvious effect on amount or kind of growth or on frequency of sector formation. When sugar was omitted, the vigour of growth was reduced, but sectors were formed, though not so frequently as on the complete medium. In the absence of peptone, growth was reduced to a thin scanty film, with no formation of sectors.

The most striking results were obtained in the experiments in which the phosphate constituent was modified. The results obtained are summarised in Table I.

Table I.

Medium	No. of plates inoculated	No. showing sectoring
1. No phosphate	147	2
Phosphate (KH_2PO_4) replaced by:		
2. K_2HPO_4	51	0
3. K_2HPO_4 + malic acid (0·1–0·16 %)	73	43
4. K_3PO_4	50	0
5. K_3PO_4 + malic acid (0·16 %) ...	20	10
6. Malic acid (0·08–0·16 %)	28	0
7. NaH_2PO_4	24	9
8. $KHSO_4$	20	0

It is clear from the above table that sector formation takes place only in media containing an acid phosphate.

The effect of acidity on sector formation was well shown in some experiments in which a glucose peptone medium was made up to different degrees of acidity or alkalinity by addition of malic acid or sodium bicarbonate. The medium normally is acid, 100 c.c. requiring approximately 0·07 gm. of sodium bicarbon-

ate for neutralisation. Nine modifications of the medium were made up, one being definitely alkaline, one neutral and the remainder showing a range of acidities. Fourteen plates of each medium were used. Table II shows the number of plates in which sectors occurred.

Table II.

Glucose peptone medium with:							
0·16 % $NaHCO_3$ (Alk.)	0·07 % $NaHCO_3$ (Neutral)	Malic acid (%)					
		0	0·005	0·01	0·02	0·04	0·08	0·16
0	0	7	9	9	6	5	2	0

(4) *Nature of the sectors produced.*

In the culture illustrated in Pl. IV, fig. 1, all the sectors proved on isolation to belong to a new strain clearly different from the parent. A considerable percentage of such sectors, however, have proved on examination merely to yield the parent form. The following data illustrate this point.

Twenty-two cultures showing sectors on glucose peptone agar (some of the plates showing more than one) were examined by transferring portions of the growing edges of the sectored areas to fresh plates of Brown's synthetic agar and comparing with cultures of the parent strain. Altogether thirty-three transfers from the growing edges of sectors were made. Of these, thirteen gave the parent form, the remaining twenty were different.

Sixteen of the saltant colonies were again transferred by taking a mass inoculum from the growing edge. The second series of cultures gave the following results:

Saltant remained saltant in ten.

Saltant reverted to parent in four.

Saltant gave rise to mixed parent and saltant in two.

Of seven similar transfers of the parent form six remained true to type, and one showed admixture with a saltant form.

In a further series of tests, cultures were grown on glucose peptone agar and transfers made from the growing edge of sectors, from the base of sectors, from the edge and from the centre of the parent colony and the resultant cultures compared. A typical set of results is shown in Table III.

Table III.

Origin of inoculum	No. of inocula taken	Saltant	Parent
Edge of sectors	15	9	6
Centre of parent colony	9	2	7
Edge of sectors	8	8	0
Base of sectors	8	4	4
Edge of sectors	30	6	24
Edge of parent colony	30	10	20

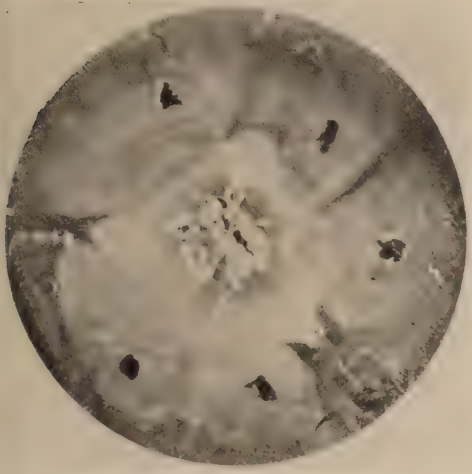
Transfers from the edge of the sectored regions give a higher percentage of saltant strains than transfers from within the body of the culture, but it is remarkable that sectors can occur, transfers from which do not give a higher percentage of saltants than are obtainable by culturing from the edge of the typical part of the culture.

It is clear that there is a great deal of admixture in these sectored cultures and that there are sectors which may be described as "false" inasmuch as they do not appear to be essentially different from the normal part of the culture, though differing very considerably in appearance. Other sectors which are indistinguishable in appearance from the preceding, however, regularly give rise to new strains when examined in the same way.

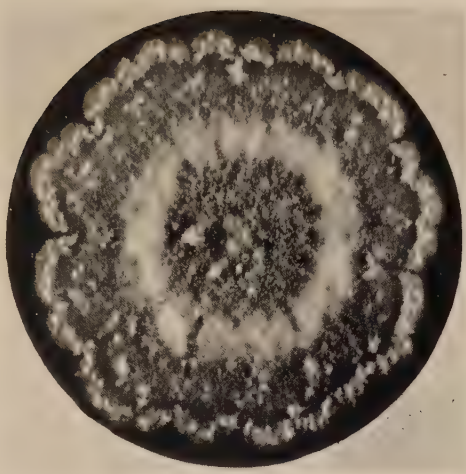
The parent culture obviously tends to throw off saltants repeatedly and these may be obtained by reculture from any part of the parent. Though the striking divergent sectors may appear on the shallow side, there is clear evidence that saltant areas are present on the deep side, though they may not give rise in the parent culture to clearly marked sectors. The device of growing the cultures on a shallow medium appears to magnify the difference between saltant and parent. It cannot be claimed that the shallow medium is the cause of saltation as such.

The appearance of highly exaggerated sectors, as illustrated in this paper, is probably capable of explanation in terms of staling phenomena. Under the conditions of culture on shallow plates and on certain slightly acid media, any portion of the growing margin which slightly outstrips the neighbouring parts gets a certain advantage and this advantage becomes cumulatively greater as time goes on. It advances further and further, and so tends still more to repress the growth of the neighbouring parts of the margin. On a deep medium the same appearance cannot arise, as there is in this case a greater development of fungal mycelium with correspondingly great liberation of staling products. On this account the whole plate is rendered unsuitable for further growth, and thus the formation of strongly outgrowing sectors is prevented. On a very shallow medium there is a minimal liberation of staling products, so that conditions are favourable for the continued growth of any part of the margin which is slightly in advance of the remainder.

From these considerations it is clear that where the sector proves to be a saltant strain, there may be very little difference in growth rate between parent and saltant. In fact a number of tests have failed to establish any definite difference in growth rate between the parent strain and some saltants derived from it. This feature is more pronounced still where the sector proves



1



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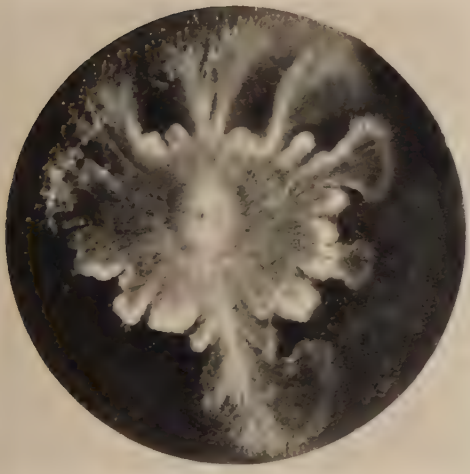

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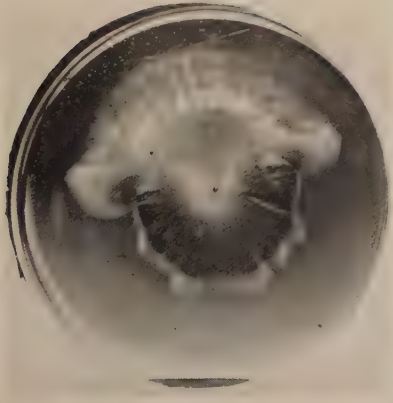

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6

on isolation to be merely the parent (*e.g.* in Pl. IV, fig. 6). In spite of the very pronounced sectored appearance shown here, which would seem to indicate the presence of a rapidly growing saltant strain, no difference whatever was observable between the normal and sectored portions when these were subsequently compared.

It might be suggested that there is a difference in growth rate between the sectored and normal portions, but that it is so small as to be masked by the experimental errors of determination. The question therefore arises whether this small difference can be increased by selective culture through a number of generations. For this purpose the following experiment was carried out.

From such a plate as is illustrated in Pl. IV, fig. 5, a transfer was made from the edge of the sector to a shallow plate of the glucose peptone medium. The resultant colony again produced a similar diverging sector. The process was repeated a third time, and again a similar sector arose. This was then carefully compared with the stock parent culture and no difference appeared. There is thus no evidence of intensification of small differences after three generations. This type of experiment has been repeated a number of times, with always the same result. Provisionally, therefore, one must consider that such sectors are false in that there are no grounds for believing that they represent saltant strains.

In conclusion, I wish to thank Professor W. Brown for his continuous interest and help throughout the course of the work.

Summary.

1. Under suitable conditions, viz. on shallow plates of medium containing an acid phosphate, certain strains of *Fusarium fructigenum* regularly give rise to strongly diverging sectors.

2. Many of these sectors do not represent saltant strains. On isolation and reculture they prove to be identical with the parent.

References.

(1) Brown, W. Studies in the Genus *Fusarium*. IV. On the Occurrence of Saltations. Ann. Bot. xl (1926), pp. 223–243.

(2) Christensen, J. J. Physiologic Specialisation and Parasitism of *Helminthosporium sativum*. Univ. of Minn. Agr. Expt. Sta., Tech. Bull. 37 (1926), pp. 1–101.

Explanation of Plate IV.

Strain *A* of *Fusarium fructigenum* Fr., on glucose peptone agar.

Figs. 1, 3, 4. Showing highly lobed, sectored appearance on shallow plates.

Fig. 2. Showing appearance on deep plate.

Figs. 5, 6. Showing sector-like outgrowths on the shallow sides of obliquely poured plates.

FURTHER STUDIES OF THE BROWN ROT FUNGI.

IV. SCLEROTINIA FRUCTIGENA AS THE CAUSE OF AN APPLE CANKER.

By H. Wormald.
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(With Plate V.)

On the variety trial plot of apples at the East Malling Research Station there are four trees of the variety known as Melon. Towards the end of August, 1928, my attention was drawn to these trees because the leaves on some of the leading shoots were withering. An examination was made to ascertain the cause and it was found that the wilting was a result of infection by the Brown Rot fungus, *Sclerotinia fructigena*. In each tree the fungus had first infected a fruit, from which it had extended into the spur, then into the branch to produce a canker, and the leaves on the parts terminal to the canker wilted in consequence.

Sclerotinia fructigena is the fruit-rotting fungus of common occurrence on apples, pears and quinces as they approach maturity, though it is also found on the stone fruits and in some years causes considerable infection of plums in this country. The fact, therefore, that this fungus, which is so very prevalent on the fruit itself, has been found to cause pronounced cankering on apple trees, appears to be worthy of putting on record. It has previously been recorded(1) as killing fruiting spurs and occasionally extending into the branches to produce cankers on the soft-wooded variety James Grieve, but in the case here recorded, on the variety Melon, the damage was more serious, from the fact that the leading branches of young trees became infected; and, as it was necessary to cut back the branches below the cankers, the general shape of the trees was impaired at a stage when careful pruning was being exercised in order to produce well-shaped trees.

It should be noted in passing that the closely related parasite *Sclerotinia cinerea* attacks branches of fruit trees, but in such instances infection takes place through the flowers, and one form of this fungus, *S. cinerea* forma *Mali*, is a frequent cause of blossom-wilt and cankers on apple trees(2), sometimes producing considerable damage by killing flowering spurs and branches.

The Melon apple, though not very well known and seldom cultivated on a commercial scale, appears to have been grown in this country for nearly eighty years. It was raised in Ontario

and introduced to the trade about 1845. In Beach's *Apples of New York* (where this variety is described as "one of the best dessert apples of its season") it is stated that "the tree is apt to be injured by canker on the limbs and on the body." The type of canker referred to is not mentioned however. *Sclerotinia fructigena* is not known in America (3), and the common American Brown Rot fungus, *Sclerotinia americana*, is not a serious parasite of apples though very destructive to peaches and other stone fruits. It would appear therefore that the Melon apple is subject to cankers other than those caused by Brown Rot infection.

This variety of apple was brought to our notice at East Malling by a fruit-grower in the Weald of Kent who spoke very highly of it, and the four trees at this station were raised by grafting from material supplied by him in 1923. The stock on which the grafts were worked was East Malling No. V (Doucin Amélioré). The trees were five years old therefore at the time these observations were made and they came into bearing for the first time that year (1928). They are growing on a plot well manured and cultivated and they have made good growth. They have been pruned in a normal way—leader tipped and long spur-pruned, the leading branches having been cut back each winter about one-third of the length of the previous year's growth. In 1928 two or three buds towards the tip of each leader developed into fruiting spurs; these spurs bore fruit and some of the buds grew out as strong vegetative shoots which served to continue the leaders. It was the wilting of the leaves on some of these leading shoots that was such a conspicuous feature of this disease.

The parasite probably entered the fruit through wounds; injuries caused by insects are frequent ports of entry for this Brown Rot fungus. The rot extended through the apple and the fungus then grew forward, *via* the fruit stalk and the spur, into the two-year-old branch bearing the spurs, producing a canker there, with the result that the current year's shoots inserted on the cankered area were killed. As the rot developed in the fruit numerous pustules of the *Monilia* stage of the fungus appeared as usual on the fruit itself, and pustules also developed on the cankered parts of the branches and spurs (Pl. V, fig. 2).

In order to ascertain the extent of the damage the trees were examined for Brown Rot infections on August 23rd, 1928, and the infected apples were counted. Tree No. 4 was smaller than the others; it bore only two apples and both were sound. The following remarks therefore apply only to the three larger trees.

A count was made of the fruit on each tree and those which had recently fallen, thus omitting small apples which had been on the ground for some time and which represented the normal early fruit fall.

Of those on the ground eleven were infected with Brown Rot and two were sound; of those on the trees, seven were infected and twenty-five sound. In the total crop of forty-five apples, therefore, eighteen (*i.e.* 40 per cent.) were infected.

Apples infected with Brown Rot often fall away from the stalk when the rot reaches the stalk end, and this explains the relatively high number of infected fallen fruit. On the other hand some infected apples may remain on the trees and gradually shrink to form the so-called "mummied" apples. This usually occurs when the infected fruits are in clusters or when they come in contact with the branch, to which they then cling, the fungal pustules growing out from the apples to form a pad, which adheres firmly to the bark at the point of contact. On August 23rd, some of the apples were already shrunken and mummified; they were nearly covered with pustules and must have been infected for some time. The following notes taken on that date show the damage caused on each of the three infected trees:

Tree No. 1. Two infected apples were on the ground. Another was attached to the branch, not only by its stalk but also by the fungal pustules at the point where the apple touched the branch; it was shrunken and mummified. Infection had extended into the branch to form a canker three inches long on the previous year's wood, thus causing the wilting of a shoot inserted on the cankered area. *Monilia* pustules were present not only on the apple but also on the canker.

Tree No. 2. Two spurs on one branch had become infected but the apples which had been borne on the spurs had fallen. Two infected apples were on the ground and it is to be presumed that they had become infected while they were still on the tree, and had fallen from their stalks, but not before infection had extended into the stalks, from which it passed into the spurs. Round the base of each of these spurs a canker about three inches long had developed on the branch. In each case the vegetative shoot which had grown out from the spur bore wilted leaves.

Tree No. 3. The terminal spur of one branch bore a mummified apple which (as in the similar instance mentioned for tree No. 1) had remained on the tree attached to the branch by the fungal pustules at the point of contact with the branch. Infection had extended into the spur and from there into the previous year's wood and also into the base of the current year's shoot. Many pustules were present on the mummy and on the cankered portions. The shoot which had grown out from the terminal bud was withering.

On another branch two apples on the terminal spur were in-

fected; these bore numerous pustules of the fungus, and pustules were also present on the spur, but as yet the infection had not produced any withering of the foliage. A second spur on this branch bore one apple, still sound at the time but in contact with one of the infected apples of the spur above.

When the tree was examined again twelve days later one of the shoots on the cankered part of this branch was withered, while the apple noted as sound on August 23rd was now infected with Brown Rot and bore numerous pustules.

Soon after the above notes were taken the infected branches were cut back below the cankers so as to remove from the trees such sources of infection. The cankered parts were not destroyed, however, but were taken to another part of the station and exposed to open-air conditions, so that the further development of the fungus on the cankers could be observed. No further development took place that year and the pustules gradually dried up, assuming the appearance of brown scars. In June the following year the fungus resumed its development on these cut-off cankers and again produced the typical yellowish pustules of the *Monilia* stage of *Sclerotinia fructigena* (Pl. V, fig. 4).

It is evident that the Melon apple is not only very susceptible to infection of the fruit by *Sclerotinia fructigena* but that the spurs and branches may be invaded by the fungus to cause cankers, and that when young trees are attacked they may be seriously damaged. James Grieve is another variety which is very susceptible to Brown Rot infection of the fruit and in this variety also the fungus may extend into the spurs and branches to form cankers, though I have never seen on James Grieve the severe cankering of branches and the killing of shoots shown by the Melon apple trees here described.

This infection of spurs and branches, with the resulting cankers on which the fungus produces its fructifications, is a factor that must be taken into consideration therefore in relation to the over-wintering of the parasite. It is now generally well known among fruit-growers that mummified apples infected with Brown Rot will serve as sources of infection the following year if they are allowed to remain on the trees. It may not be realised, however, that cankered spurs and branches may serve a similar function in the interests of the parasite.

Reference has been made to cankers caused by *Sclerotinia cinerea* forma *Mali* on apple trees. This fungus does not produce fructifications on the cankers (though they may be found on the flowers and the axis of the inflorescence) during the summer in which infection occurs, but pustules appear the following winter and spring; they may be seen in December and they continue

to develop until the tree comes into blossom, when infection of the flowers occurs.

In *S. fructigena*, on the other hand, pustules appear on the fruit and cankers during the period of infection (August and September); these cease to function on the approach of winter and a fresh crop of pustules does not appear until the following May or June. This late appearance of the fructifications of *S. fructigena* is correlated with the fact that this fungus is essentially a fruit-rot organism and is not known to infect the flowers.

While the above account was being prepared for publication Mr S. P. Wiltshire informed me of an outbreak of Brown Rot on an apple tree in his own garden at Kew in September, 1929, and kindly sent me specimens. Here again *S. fructigena* had first infected the fruit and from the fruit had extended into the spurs and branches, pustules appearing on all the infected parts. The variety of apple was not known but it proved to be neither James Grieve nor Melon.

Furthermore in October, 1929, Mr M. H. Moore drew my attention to a Brown Rot canker on a tree of Cox's Orange Pippin on the spraying trial plot on this station. It was seen that, in this instance also, the infection had begun in an apple, which had fallen after the fungus had reached the spur. From the spur the infection had proceeded into the branch, which at that level was more than half an inch in diameter, and had produced a canker two inches long, almost girdling the branch, and bearing a few conidial fructifications of *S. fructigena*.

The Melon apple trees bore but little fruit in 1929 and consequently there was little infection on them; however, a canker with fructifications of *S. fructigena* was found on each of two of the trees when examined in October, 1929. Near them a canker of the same kind was present on a tree of a variety known as Cutler Grieve.

Thus Brown Rot cankers following infection of the fruit by *Sclerotinia fructigena* have been observed on five varieties of apple.

Summary.

A description is given of a severe infection of Melon apple trees by *Sclerotinia fructigena*.

Not only was the fruit infected, but the infection extended into the spurs, and also into the branches to cause cankers. These cankers girdled the branches and killed the parts terminal to them.

Monilia pustules appeared on the infected parts during the period of infection (August); these ceased to function on the

1

2

3

4

approach of winter but another crop of pustules appeared the following June.

Brief reference is made to similar infection on four other varieties of apple.

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DESCRIPTION OF PLATE V.

Fig. 1. A wilted shoot of the Melon apple infected with *Sclerotinia fructigena*.
Fig. 2. The apple and canker of Fig. 1, showing the *Monilia* fructifications on the fruit and on the canker.
Fig. 3. Cankers on this branch were caused by infection from two apples, which have fallen. The two shoots on the left are dead and each has a canker at the base.
Fig. 4. Cankers, which were the result of infection in August, 1928, bearing conidial pustules of *S. fructigena* in July, 1929.

STUDIES IN THE MORPHOLOGY OF DISCOMYCETES.

III. THE CLAVULEAE.

By E. J. H. Corner, B.A.

(With three Text-figures.)

There is a form of stipitate ascocarp in the Inoperculeae which differs so markedly from the usual stipitate apothecium that it requires special consideration. It is the monaxial clavate ascocarp in which the upper part is covered by the hymenium and the lower part forms a stem, covered, at least when unexpanded, by a sterile palisade layer, the cortex. The form occurs in several genera which are classed by Boudier in the families Leotiaceae and Geoglossaceae in the subsection Clavuleae. In the Leotiaceae the fertile, capitate part overlaps the apex of the stem from which it is separated by a groove, whereas the two are outwardly confluent in the Geoglossaceae.

Several investigations have been made on various members of the group but they have dealt mainly with the origin and development of the sporophytic system and grosser features of the sterile tissue. I have examined the structure of the mature

ascocarp in several members of each family, and the development of the sterile hyphal system in four species, *Mitrula pusilla* (Nees) Fr., *Microglossum viride* (Pers.) Gill., *Geoglossum difforme* Fr. and *Trichoglossum hirsutum* (Pers.) Boud. The results concur sufficiently to formulate a morphological series connecting the clavate and the ordinary stipitate forms of ascocarp.

Mitrula pusilla.

The mature ascocarp is capitate, 1 cm. high at most: the head is oval, 1–1·5 × 0·5–1 mm., and separated by a groove from the slender stem, 0·2 mm. wide. The structure of the head and apex of the stem is shown in Fig. 1 (*d*). The stem is hollow, the narrow cavity being continuous with that of the head; both contain air. The wall of the stem is composed of hyphae arranged longitudinally in three layers, a surface layer of 1–2 hyphae, 3–4 μ wide, which bear pyriform cells, 15–25 × 8–10 μ, singly or in groups, scattered over the surface, a middle layer of hyphae, 5–12 μ wide, and an inner irregular layer of hyphae, 3–4 μ wide lining the cavity: there are no secondary interweaving hyphae. The hyphae of the head are 5–10 μ wide; they form loose strands radiating from the stem apex through the peripheral part of the cavity and ending in sympodial clusters of paraphyses, 3–4 μ wide. But the lowest hyphae are arched over the groove from the stem apex to the margin. The underside of the head, in the groove, is lined by a cortical layer of short rows of two to three, more or less isodiametric cells, 7–15 μ, oblique to the surface. The cortical hyphae are derived from a small marginal growing-point and at the stem apex they are reduced to single cells forming a transition to the scattered pyriform cells. The apical cells of the paraphyses and of the cortical hyphae, as also the pyriform cells, contain a yellow vitreous substance which, with the pale brown walls of the outer hyphae, causes the yellow-brown colour of the fruit body.

The structure of the youngest stage examined is shown diagrammatically in Fig. 1 (*a*); it is a shaft of 2–4 μ hyphae, 200 × 100 μ. The hyphae form a monopodial system; those in the centre grow apically and, while the growth of those on the outside slackens, their apical cells enlarge and become pyriform, and their place in the growing point is taken by laterals. The pyriform cells cover the whole shaft except, of course, at the apex and at the base where secondary mycelial hyphae, 2–3 μ wide, grow out: new pyriform cells are intercalated sympodially.

Upgrowth of the shaft continues until it is 300–400 μ high, and about 130 μ wide, when the distal parts of the upgrowing hyphae in the centre are transformed into paraphyses and the

development of the hymenium begins. But at the margin a growing-point is established; it is active only for a short time

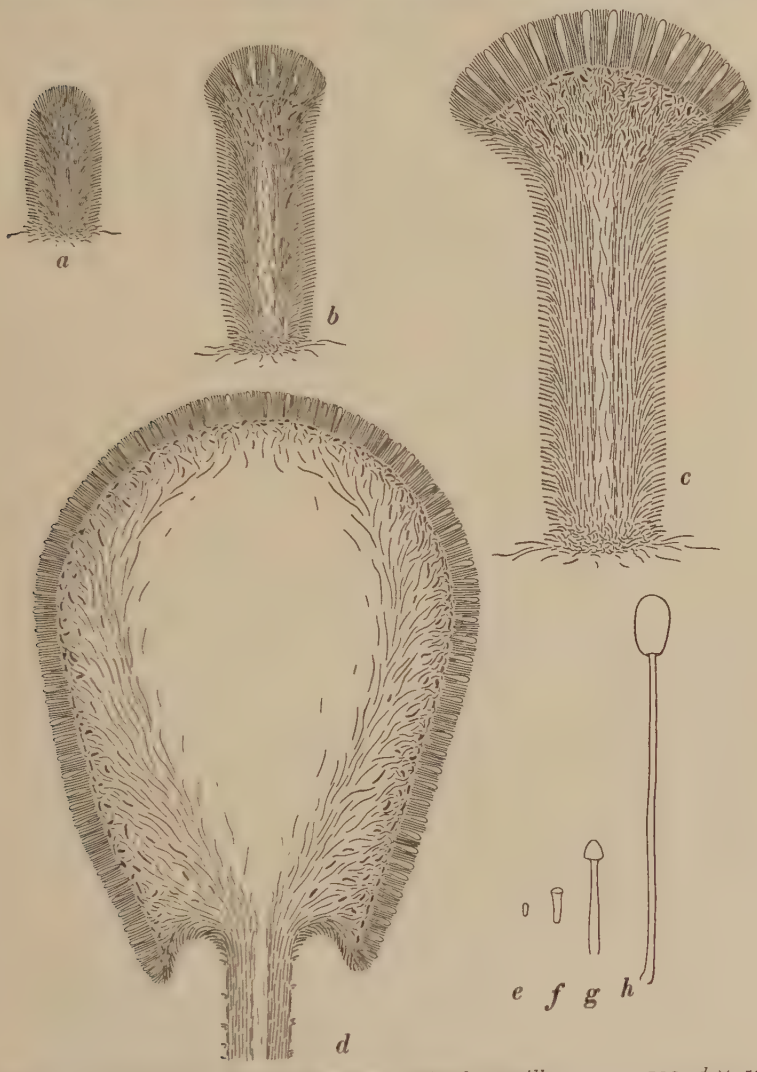

Fig. 1. Development of the ascocarp, *Mitrula pusilla*. *a–c* × 100, *d* × 50; *e–h* × 5; *b*, *c* = *e*, *f*. *b*, upgrowth ceased and asci develop; *c*, asci mature.

and consists of the ordinary sympodium. Young asci appear in the hymenium shortly after upgrowth ceases, stages (*b*) and (*c*); they first appear in the centre, then at the periphery, which

suggests a radial growth of the ascogenous hyphae in company with the margin. The ascogenous hyphae can be traced back to four or five knots of closely coiled hyphae, 4–5 μ in width, situated internally where the stem expands into the head, and rather wider than the surrounding hyphae. These knots of hyphae were not found in stages such as *a*, and they possibly represent ascogonia, though their detailed structure could not be made out.

Enlargement of the hyphae in the stem region begins shortly before cessation of upgrowth. The motor tissue is a broad cylinder of hyphae just within the surface and not including the central hyphae, which are therefore pulled apart to form the cavity of the stem. The motor tissue forms the middle layer of the mature stem, the height of which is due mainly to elongation of the cells, which are at first *ca.* 10 μ long but finally 30–100 μ. The covering of pyriform cells splits up during elongation and forms the scattered tufts on the surface.

The head passes rapidly through a disc stage, *c* and *f*, about 1000 μ high, when marginal growth ceases and spore discharge begins. Further enlargement of the head is due entirely to intercalary growth of the hymenium, which arches the upper surface, pulling the underlying hyphae apart and causing the air cavity. The head passes from a lenticular shape through a conical to the final "cucullate" shape. The hymenial growth presses the underside of the apothecial part over the stem, compressing the cortical cells, which thus support the turgid hymenium.

I have found that the ascocarps of *Mitrula sclerotipus* and another unnamed species, *Leotia lubrica* and *Cudonia circinans* have the same structure. In the last two, however, it is difficult to decide if there is a marginal growing-point or if the underside of the head is simply the dilated apex of the stem; and in these species the intercalary growth of the hymenium is irregular. In *Cudoniella acicularis* the marginal growth is relatively greater and intercalary growth of the hymenium relatively less than in the other species, which causes the ascocarp to occupy a position intermediate between the Helotiaceae and Leotiaceae.

Duff (3) has examined *Cudonia lutea*, and judging from his illustrations there must be considerable marginal growth of the apothecium. The fruit body develops within a veil, the hymenium forming in a subapical mucilage space. The veil is eventually ruptured and remains in patches round the margin of the apothecium; details of the hyphal system are lacking, though it appears similar to what the writer has found in *Microglossum viride*. Dittrich (2) describes a veil also in *Leotia lubrica* but it was not seen by Duff nor by Brown (1), who gives a diagram of the structure of the mature ascocarp.

In *Mitrula phalloides*, according to Dittrich (2), there is an initial shaft of hyphae, as in *M. pusilla*, which reaches about 1·5 mm. high before upgrowth ceases and the formation of the hymenium begins. But the growth continues at the margin, which arches over the apex and forms a dome of tissue overlying a mucilage space in which the hymenium continues to develop. The dome of tissue becomes mucilaginous and is ruptured by the hymenial growth, which finally causes the clavate shape of the head, as in *M. pusilla*, and forces the margin back over the stem. There does not appear to be any cortical layer in this species, for all the surface tissue becomes mucilaginous and forms a veil. The structure of the mature ascocarp, however, is very like that of *Microglossum viride*. The head is elevated by elongation of the stem region.

Microglossum viride.

The mature ascocarp is 3–4 cm. high, solid and clavate, though the fertile region is clearly distinguishable from the stem as a darker green, thicker, more or less flattened, distal part. The structure of the ascocarp at the junction of the stem and head is shown in Fig. 2*e*. The tissue of the head is homogeneous, consisting of more or less contiguous, longitudinal hyphae, 3–8 μ wide, mostly 5–6 μ, with a few interweaving hyphae 3–5 μ wide: the hyphae end in tufts of paraphyses 2–2·5 μ wide. The structure of the stem is similar, but there is a surface layer, two to four hyphae deep, of rather short-celled hyphae, 8–12 μ wide, often with rough walls: the layer may be continued for a short distance into the head immediately internal to the hypothecium. Tufts of short hyphae, of one to two cells, arise from the outer layer of the stem: they are 7–10 μ wide, with the same rough walls, and their tips are usually agglutinated in greenish mucilage. At the junction of hymenium and stem the paraphyses become progressively shorter, on passing downwards, and gradually assume the characters of the hyphal tufts on the stem: the ascogenous hyphae do not approach within 100 μ or so of the transitional region, but in certain parts, usually on the narrow sides of the flattened head, the structure of the transitional region is different. The paraphyses become shorter but their proximal cells enlarge to 5–8 μ wide, and in the lowest paraphyses—all but the apical cell, which remains narrow—2–3 μ. These hyphae have not arisen directly from the hypothecium but have grown from some higher point, for their course is curved down over the apex of the stem. They have the appearance of belonging to a marginal growing-point which has been reflexed by hymenial pressure, but unfortunately they could not be recognised in young ascocarps. Such transitional

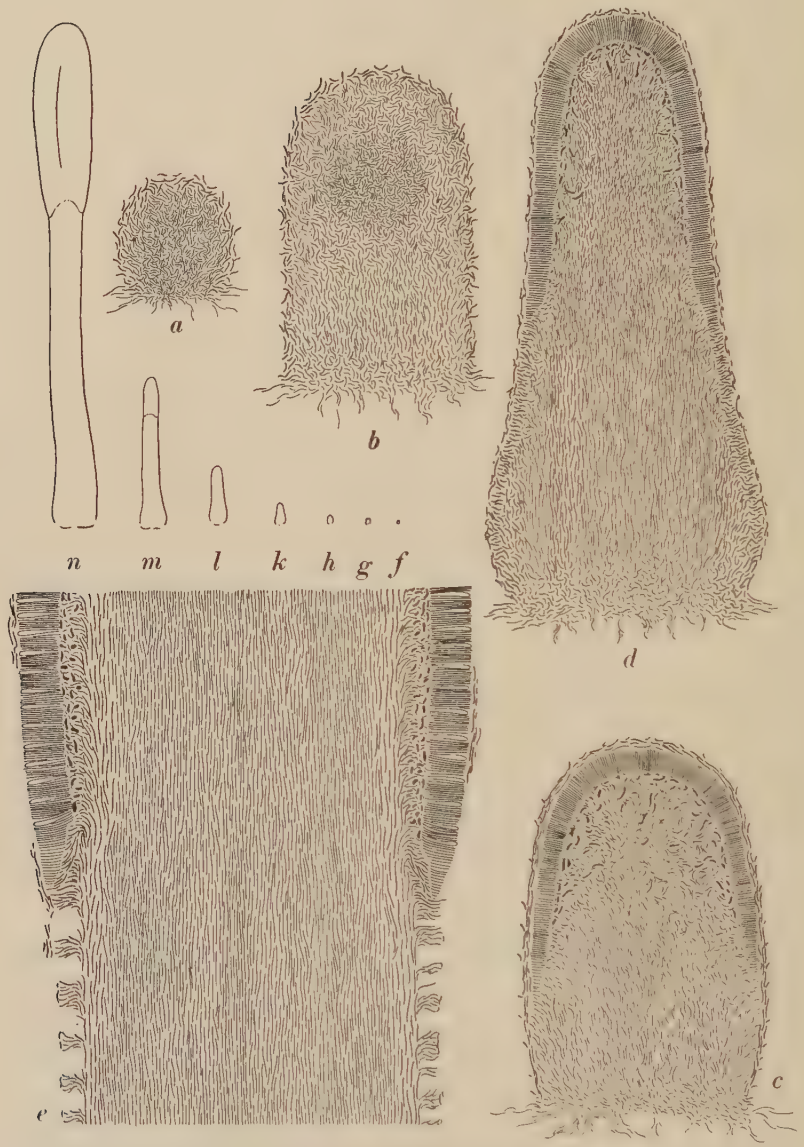

Fig. 2. Development of the ascocarp, *Microglossum viride*. *a–c* × 100, *d* × 50, *e* × 25, *f–n* × 2. *a–d* = *f–k*.. *k*, asci develop; *m*, asci mature.

regions are shown in the diagram. Ordinary hyphal tufts occur on the stem immediately below the down-curved hyphae. The green colour of the ascocarp is due to the yellowish green walls of the hyphae.

The development is complicated and difficult to follow owing to the very large number of hyphae involved, about 100,000 in a stem 2·5 mm. wide, and to their small size, compactness and sinuous course in early stages; but the main points are clear.

The earliest stage examined was a globose dark green body, 150–200 μ wide, composed of a central mass of densely interwoven hyaline hyphae, 2–3 μ wide, forming a tissue devoid of air spaces, and an outer covering, two to four hyphae thick, the hyphae 4–6 μ wide, with rough yellowish green walls, stage *a*. Such a structure implies an antecedent condition in which all the hyphae are similar, 2–3 μ wide, and that the outer covering is due to the modification of the outer hyphae on cessation of upgrowth. The primordium continues to enlarge by branching of the hyphae, especially just within the outer layer, which persists as a definite investment or veil throughout the early stages of development. Growing hyphae can also be seen in the veil itself, suggesting that it continues to extend by intercalary growth.

The primordium begins to lengthen owing to the enlargement of the basal hyphae, not to any special upgrowth, and when it is about 300–400 μ high, stage *b*, a knot of densely interwoven hyphae with granular contents appears a little above the centre in the internal tissue. The origin of the knot is obscure, but as several unusually wide, 5–8 μ, short-celled hyphae occur in the middle and the granular hyphae are clearly growing towards the periphery, the knot may represent the origin of the ascogenous hyphae from ascogonia. Numerous growing hyphal tips occur over the upper part of the primordium just internal to the veil.

At a later stage, *c*, when the primordium is 500–800 μ high, enlargement of the basal hyphae continues, but the central knot has disappeared and a palisade layer of narrow, 2 μ, hyphae has formed over the upper half, internal to the veil. The palisade layer first appears over the apex but proceeds downwards near the base where the number of outgrowing hyphae is few and their course is more irregular. It is impossible to decide whether the palisade hyphae are still growing at this stage, because there is no visible means of distinguishing them from paraphyses. What are evidently ascogenous hyphae can be seen at this stage worming their way between the proximal parts of the palisade hyphae.

However, in stage *d*, which is about 1500 μ high, upgrowth

of the palisade layer has certainly stopped, because a few young asci have been formed over the apex. In the basal half of the primordium the outgrowing hyphae have assumed the appearance of the cortical hyphae which form tufts on the surface of the mature stems: the transformation follows on cessation of growth and numerous laterals are intercalated, which may grow in almost any direction up or down or straight out and produce in turn tufts of cortical hyphae. The growth of the ascogenous hyphae, as shown by the appearance of asci in the hymenium, proceeds from the apex to the transitional region. The asci, however, do not mature until the fruit body is 10–15 mm. high, stage *m*, except in stunted specimens which may not reach more than 5–10 mm.

Elongation of the primordium is due to the extension of the hyphae in the head and stem region and to the intercalary growth of the hymenium in the head which elongates about fifty times its original length. The process of elongation, which proceeds acropetally from an early stage, is remarkable, though widespread in basidiocarps with indirect development, because the hyphae, which are closely interwoven in the primordium but in alignment in the mature fruit body, must slip over each other as they straighten out, and none, apparently, get inextricably entangled.

Elongation of the stem splits the veil and cortical layer transversely into patches. The veil, however, owing to dissolution of the hyphae at an early stage, is at this period no more than a mucilaginous pellicle covering the primordium, and patches of it may persist for some time as green flecks on the stem and hymenium.

Intercalary growth of the hymenium may be uniform or it may be greatest on two opposite sides of the head, causing it to be flattened, and on these sides the hymenium is usually continued further down the stem than on the flat surfaces.

The endogenous development of *M. viride* has already been noted by Durand (4), and from Duff's account (3) the development of *Spathularia velutipes* must be similar. It is endogenous in a veil, and the structure of the mature hyphal system, from Lagarde's description (5), is similar, but the mature ascocarp differs markedly in the much-flattened fertile region which appears to descend the stem on the two narrow sides. Developmentally the appearance must be ascribed to the failure to form the hymenium on the lower part of what subsequently becomes the broad sides of the head. The appearance is common in clavate forms but is rarely so marked. Patouillard has described a form, *Hemiglossum*, in which apparently no hymenium is formed on the whole of one side of the head, which suggests that

another may exist with two hymenial surfaces separated by a longitudinal strip of sterile tissue: the development of transverse strips of sterile tissue is not known in Inoperculeae, cf. *Morchella*.

Geoglossum difforme.

The mature ascocarp is typically clavate, more or less flattened, 5–7 cm. high. The structure is similar to that of *Microglossum viride* but there is no trace of a marginal growing-point and the transition between sterile and fertile regions is imperceptible externally: the structure of the transitional region is shown in Fig. 3*d*. The tissue of the head is homogeneous, the hyphae being longitudinal, 7–15 μ wide, and with few, 3–6 μ, interweaving hyphae: in the centre the hyphae are pulled apart by the growth of the hymenium and form a loose tissue with air spaces. The paraphyses are flexuous, especially in the distal part, mucilaginous, colourless, 2–4 μ wide in the basal part, but with brown walls above and with the distal two or three cells enlarged, 4–6 μ in diameter, and short. The longitudinal hyphae of the stem are in three layers, a narrow outer layer of hyphae, 3–6 μ wide, and a broad intermediate layer of hyphae, 7–15 μ wide, which is the chief motor tissue, and a narrow central core of hyphae, 3–6 μ wide. The stem is covered by a cortex of hyphae similar to the paraphyses though rather shorter; they are connected with the outer layer of longitudinal hyphae and are usually separated into indistinct groups by the elongation of the stem. A peculiar feature of the stem is the abundant development of interweaving hyphae, 3–6 μ wide, which ramify irregularly in all directions between the main hyphae and which if they reach the cortex may give rise to clusters of cortical hyphae. The black colour of the ascocarp is due to the dark brown walls of the hyphae, the only colourless walls being those of the asci and mucilaginous portions of the paraphyses.

Development is simple and direct. The earliest stage examined was a monopodial, corticated shaft of 2–3 μ hyphae, 400 × 200 μ (Fig. 3*a*). The upgrowing hyphae have a flexuous course, which is reflected in the dense interwoven tissue of the primordium. Laterals arise some distance below the apex of these hyphae so that a palisade layer covers the primordium, except at the base where secondary, 2–4 μ wide, brown mycelial hyphae arise. The cortex is composed of the distal parts of the outer hyphae of the shaft, which cease growing and branch sympodially; branching is also restricted to the proximal cells, and cortical filaments may be added from hyphae which have originated more internally. Apparently there are many of these deep-seated laterals which worm their way to the surface by devious routes, arriving at points widely separate from the

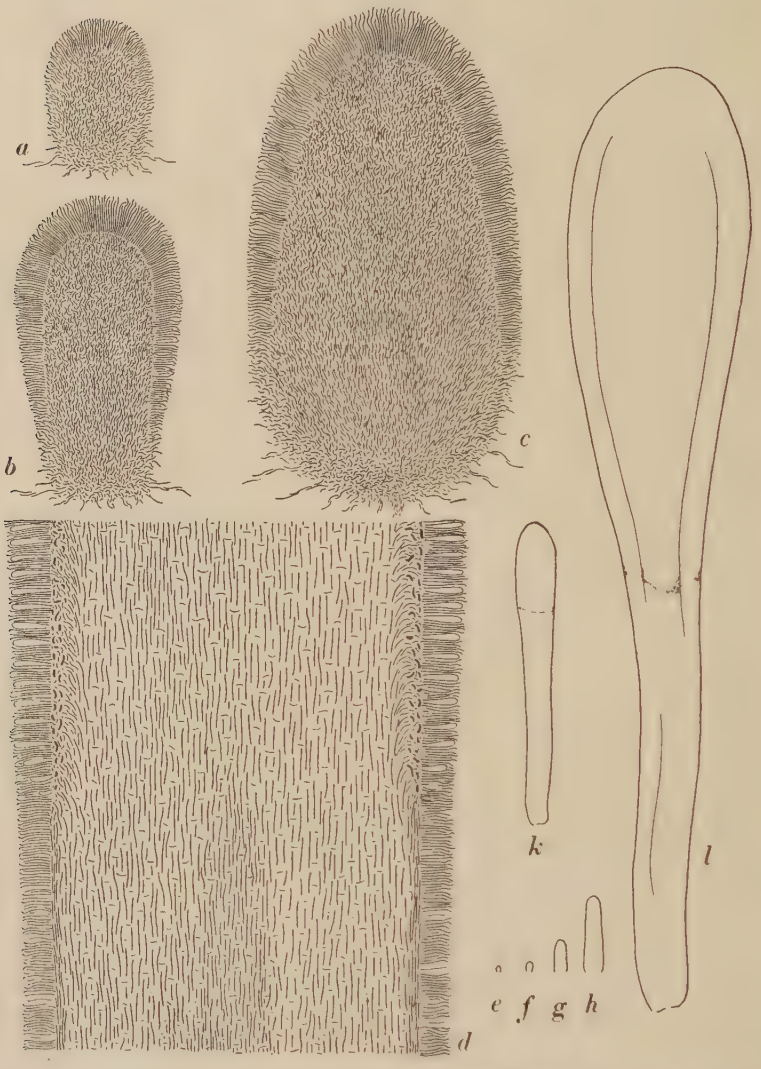

Fig. 3. Development of the ascocarp, *Geoglossum difforme*. *a–c* × 50, *d* × 25, *e–l* × 2. *a*, *b* = *e*, *f*. *c* and *g*, upgrowth ceased; *h*, asci develop; *k*, asci mature; *l*, mature ascocarp.

parent hyphae, which renders difficult the unravelling of the hyphal system. In stage *b*, the hyphae in the basal part of the primordium have begun to enlarge and straighten, as in *Microglossum viride*, and the process continues acropetally till

maturity. Upgrowth ceases apparently when the primordium is 1·5–2 mm. high, stage *g*, and all the apical hyphae are distinctly paraphysoid, but it is difficult to decide this exactly. Asci do not appear in the hymenium till the primordium is 5–8 mm. high and do not mature till it is about 20 mm. high, stages *h* and *k*. The asci appear first over the apex, as in *M. viride*, and then progressively to the lower limit of the hymenium, implying a similar downgrowth of the ascogenous hyphae.

Elongation of the primordium takes place as in *M. viride* and to about thirty to forty times the initial height. Intercalary growth is usually greatest on opposite sides of the head, which causes the flattening of the fertile region.

The primordium of this species is formed at depths of 0·5–2 cm. in the soil among the roots of grasses and the period of upgrowth probably depends largely on the depth of origin. If the soil is hard and stony, the primordium twists between the particles of earth, which causes the frequent curly base of the stem. The specimens examined came mostly from a depth of *ca.* 0·5 cm.

Trichoglossum hirsutum.

The mature ascocarp is not typically geoglossoid, for the fertile region is clearly delimited as a thicker portion from the stem, and in the capitate variety the fruit bodies have the appearance of miniature gong sticks, 6–8 cm. high. This is due to the greater limitation of the hymenium and relatively greater intercalary growth, much as in *Mitrula*, *Leotia*, etc. Nevertheless, the structure and development are essentially the same as in *Geoglossum difforme*, the only noteworthy differences being that many of the upgrowing hyphae mature into dark brown, thick-walled, acute, septate hairs over the whole surface, as modified paraphyses and cortical filaments, and that the cortical filaments are short, irregular, and do not form a definite pile over the surface of the stem. In a batch of fruit bodies, the largest of which were not more than 4 cm. high, many primordia in various degrees of development were found, and it was discovered that upgrowth of the primordium ceased when about 1 mm. high, and asci were matured very soon after when only 2 mm. high.

The development of this species has been examined already by Durand (4) and Duff (3) and their accounts agree with the writer's in the absence of a veil. Durand also states that a veil is absent in *Geoglossum glabrum*, *G. difforme* and *S. velutipes*, and distinguishes two kinds of geoglossoid ascocarp, namely that in which the cortical hyphae are paraphysoid (*Gleoglossum*) and that with indistinct cortical hyphae similar to *T. hirsutum*, considered as *Geoglossum* proper.

Discussion.

There are four points which require consideration. Firstly, the capitate ascocarp of the Leotiaceae differs from the ordinary stipitate apothecium only in the restriction of marginal growth and the increase in intercalary hymenial growth. In all cases, with the possible exception of *Spathularia*, the hymenium is surrounded by a definite apothecial margin and it is limited to the distal end of the primary shaft of hyphae. But in the clavate ascocarp of the Geoglossaceae there is no marginal growing-point and the ascocarp is evidently equivalent merely to the primary shaft itself, of the stipitate apothecium, over the whole upper half of which the hymenium is spread. One can formulate a series therefore which leads from the ordinary stipitate ascocarp to the clavate by loss of marginal growth, or conversely, from the clavate to the stipitate, by arrest of upgrowth, localisation of the hymenium and establishment of a marginal growing-point, as a means of broadening the apex. *M. viride* appears to be intermediate if it really has a rudimentary growing-point at the margin of the hymenium. A clavate ascocarp with localised hymenium, as in *T. hirsutum*, is also the intermediate in either case.

Secondly, the series may be traced on angiocarpic lines, cf. *Cudonia lutea*, *M. phalloides*, *M. viride*, or on gymnocarpic lines, cf. *M. pusilla*, *Geoglossum*. But the significance and even the morphological nature of the veil are obscure. In *M. viride* the veil appears to be the surface layer of a primary system of hyphae on which the secondary system of the ascocarp is spun, as in angiocarpic basidiomycetes, *e.g. Amanita*, though far less elaborate; the primary system suggests a preliminary storage organ which enables material to be concentrated from the mycelium, like a sclerotium. The veil appears of the same nature in *C. lutea*, as already mentioned, but in *M. phalloides* the part of the veil over the hymenium is said to be derived from the apothecial margin and thus is of a different category.

Thirdly, all clavate ascocarps develop indirectly in that a period of apical growth and branching in a primordium is followed by a period of enlargement of the hyphae and extension of the primordium. The only stipitate apothecia known, in fact, which may develop directly, growth and enlargement being contemporaneous, belong to the inoperculate group Ciboriaceae. I have not examined any such species but Woronin (6) describes the apothecium of several species of *Sclerotinia* developing on the top of a long stalk, not in a primordium. It is possible that *C. acicularis* is also an exception in this respect. The ascocarp of the Clavulcae thus resembles that of the Helvellaceae in general

mechanism but differs in detail, for in the Clavuleae the motor tissue of the stem is in the medulla, internal to the cortex, which is disrupted, and in the Helvellaceae it is the cortex itself, the medulla being passively stretched. The difference reveals from another aspect the impropriety of the old idea of Helvellales to embody both operculate and inoperculate forms of stipitate ascocarp.

Fourthly, the apothecia of the Clavuleae appear to be compound in that the ascogenous hyphae are derived from several ascogonia. Duff found a large number of ascogonia in the apex of the primordium of *C. lutea* and *S. velutipes*; in *C. lutea* they were coiled with multiseptate "trichogynes" which protruded through the veil but in *S. velutipes* they were merely irregular enlarged cells. According to my observations there may be several ascogonia in *M. pusilla* and *M. viride*, but the appearance of the "knot" in this species leads to the consideration of a system of generative hyphae which Duff has described. In *C. lutea* and *S. velutipes* certain deep-staining hyphae are said to appear in the primordium at a very early stage; they grow up in the internal tissue with the sterile hyphae and produce laterally the ascogonia about the time of formation of the hymenium. Duff considers that the three or four "ascogenous" hyphae, which Brown describes as growing up from the base of the primordium of *L. lubrica* from an early stage, are really generative hyphae which produce ascogonia in the apical tissue, the ascogonia being the subhymenial "storage-cells" of Brown. Likewise the subhymenial "storage-cells" described by McCubbin in *Helvella elastica* are considered ascogonia. A system of generative hyphae may also exist in *M. phalloides*, for Dittrich describes the origin and upgrowth of the "ascogenous" hyphae in the primordium from a very early stage. The generative hyphae form a deeply staining knot in the centre of the primordium in *C. lutea*, which suggests a similar nature for the knot in *M. viride*, but in this species no cells were seen in the subhymenium which might have been ascogonia.

In *Geoglossum* and *Trichoglossum* no ascogonia were seen either by Duff or myself, but Duff says that the ascogenous hyphae orginate from sterile hyphae in the subhymenium in *T. hirsutum*. He considers that there is a series leading from the well-developed archicarps of *C. lutea* through the "storage cells" in other species to the vegetative origin of the ascogenous hyphae in *Trichoglossum*, and similar to the degeneration of the archicarp in Humariaceae.

So far from having the simple organisation which the outward appearance suggests the clavate ascocarp may thus be among the most complex, for as many as four systems of hyphae, two

sterile and two fertile, may be involved in angiocarpic development.

Summary.

The development of the clavate form of ascocarp is described in *Mitrula pusilla*, *Microglossum viride*, *Geoglossum difforme* and *Trichoglossum hirsutum*. Development is indirect, and angiocarpic in *M. viride*, gymnocarpic in the others. There is a primordial corticated shaft of hyphae, at the distal end of which the hymenium forms on cessation of upgrowth. In *M. pusilla* the hymenium is limited to the extreme end of the shaft and is supported by a small pseudoparenchymatous cortex, lining the groove, formed from a rudimentary marginal growing-point. In the others the hymenium is formed over the distal half of the shaft and is not bounded by a definite margin, though there are possible traces of marginal growth in *M. viride*.

Probably all clavate ascocarps of the Leotiaceae resemble *M. pusilla* in having rudimentary marginal growth and excessive intercalary hymenial growth. The clavate ascocarp of Geoglossaceae corresponds to the primordial shaft.

The motor tissue of the stem of Inoperculeae is in the medulla in contrast to Operculeae where it is in the cortex.

The relation of the clavate form to the stipitate apothecium is shown and the systems of sterile and fertile hyphae in the clavate form are discussed.

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STUDIES IN THE MORPHOLOGY OF DISCOMYCETES.

IV. THE EVOLUTION OF THE ASCOCARP.

By E. J. H. Corner, B.A.

(With one Text-figure.)

THE gametophytic system of the ascocarp has already been described (10) so far as existing knowledge allows. In the present paper a hypothesis is proposed of the evolution of the system, but the bearing of the hypothesis on current views of the evolution of Discomycetes will be considered later.

The minute perithecioid form of ascocarp found in *Neotiella Crozalsiana* has been interpreted elsewhere (9) as a persistently juvenile form of angiocarpic apothecium. What then is its antecedent? In the second paper of this series the different forms of monaxial ascocarp have been shown to constitute a developmental series, the whole of which is embodied in the ontogeny of the stipitate apothecium. The hypothesis is therefore proposed that the simpler forms of ascocarp have devolved from the stipitate apothecium by juvenescence, that is by premature cessation of growth and precocity in reproduction. Premature cessation of upgrowth of the primordial shaft in the stipitate cupular form makes substipitate and sessile forms by reduction of the axis: premature cessation of marginal growth in the sessile forms makes the lenticular if uniform, and the auriculate if unilateral. The absence of a secondary period of development makes the turbinulate and cleistocarpic forms on angiocarpic lines, with the perithecioid as an extreme case of depauperate xerophytic mechanism, the immarginate on gymnocarpic lines and the minute lenticular on hemi-angiocarpic lines.

As the development of the ascocarp implies increase in size, so the evolutionary process of juvenescence implies decrease, and the length of the stem and the width of the apothecium measure roughly the degree of degeneration: the smallest ascocarps are at once the most juvenile and the most degenerate. But to appreciate the extent to which the ascocarp may degenerate, and at the same time the problem of the gametophytic system, some notion of the amount of tissue in the large forms compared with the small ones is essential. For this purpose certain mature ascocarps, belonging mostly to common species, have been drawn to scale in the accompanying figure:

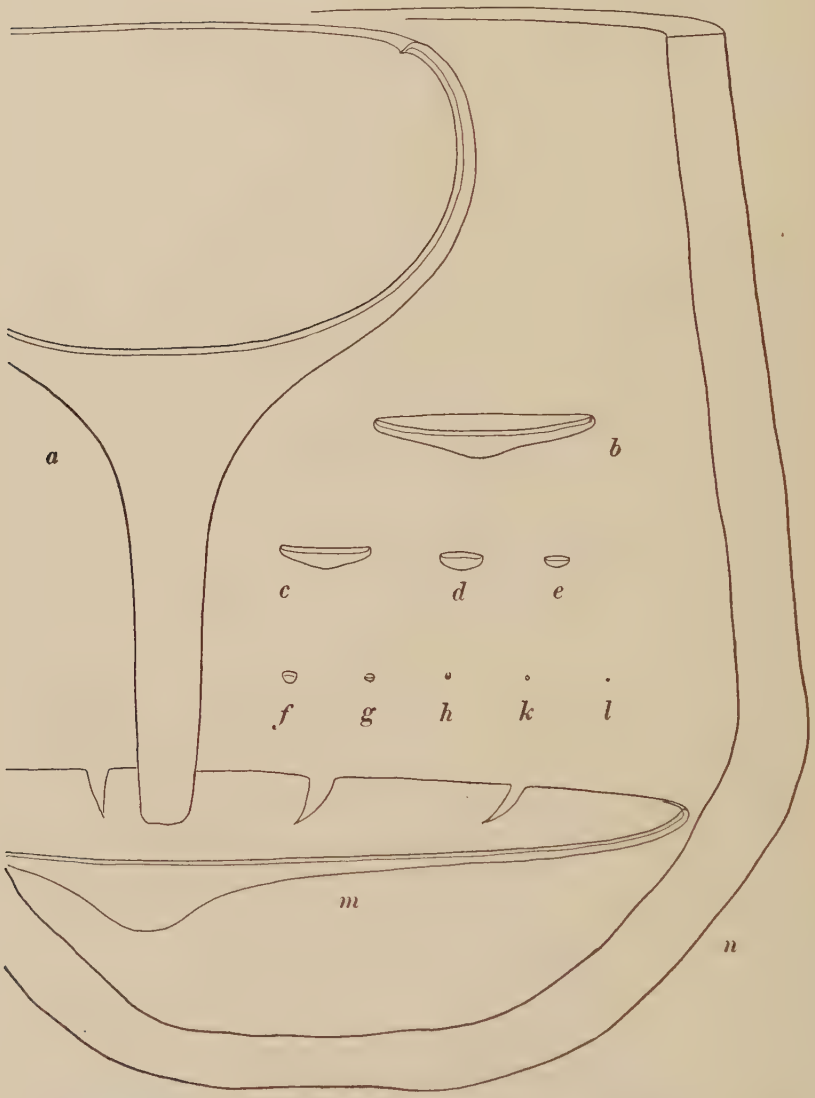

Fig. 1. To illustrate the proportions of the ascocarp; *a, Sarcoscypha coccinea*; *b, Melastiza miniata*; *c, Anthracobia melaloma*; *d, Coprobia granulata*; *e, Ascophanus carneus*; *f, Pyronema confluens*; *g, Ascophanus granuliformis*; *h, Neotiella Crozalsiana*; *k, Thelebolus stercoreus*; *l, Ascodesmis nigricans*; *m, Peziza aurantia*; *n*, the base of the stem of *Morchella crassipes*. All × 2.

they may be compared with the stages in the development of the apothecium of *Peziza aurantia* (11). The largest monaxial ascocarps may be 30 cm. high, *e.g. Morchella Smithiana* according to Cooke (8); and the largest apothecia may be 15 cm. wide, *e.g. Disciotis venosa* according to Rehm (20); while the smallest, that of *Ascophanus minutissimus* according to Boudier (3), is only 100μ high and wide. The range in length of the ascocarp, 3000 : 1, and in width, 1500 : 1, is comparable with the range in length and width of the axis in flowering plants, though on a minor scale, and stipitate apothecia, 5 cm. high on the average, and small lenticular, 1 mm. high on the average, are similarly in proportion, 50 : 1, of tree to herb.

To review the phylogeny of Discomycetes from this aspect is impossible owing to the artificial basis of classification, and the lack of knowledge appropriate to a natural rearrangement. But certain operculate series which have already been described (11), may briefly be mentioned again with some other points of classification. In the humariaceous series the ascocarp ranges from stipitate cupular to minute lenticular and perithecioid forms, 0·5 mm. wide. The cupular genus *Peziza* differs from the lenticular genus *Humaria* only in size, cf. *P. aurantia* and *H. calospora*, so that *Humaria* may be considered a depository for juvenile pezizoid forms of no immediate relationship. Possibly another subseries with pilose apothecia runs through *Peziza* from stipitate forms in *Sarcoscypha* to lenticular forms in *Neotiella*, whence the step from such an apothecium as that of the bryophilous *N. Hetieri*, 2 mm. wide, to the final perithecioid form in *N. Crozalsiana* is small, cf. *Aleuria Ricciae* (9). In the helvelloid series the ascocarp ranges from stipitate forms, 10 cm. high, *e.g. Helvella crispa*, to sessile cupular forms, *e.g. Acetabula leucomelas*. In the Aleurieae it ranges from substipitate cupular to large lenticular forms, 1 cm. wide, on several lines distinguishable by the shape and guttation of the spores, *e.g. Galactinia, Aleuria, Plicaria*. In the series *Sepultaria–Lachnea–Trichophaea* it ranges from sessile cupular to minute lenticular forms, 1–2 mm. wide, *e.g. T. Woolhopeia*.

Juvenescence can also be recognised in forms of ascocarp without a secondary period of development from the variation in size at maturity in different species. It is caused by variations in intercalary hymenial growth, mainly in the extent of the sporophytic system, and in the growth of the investing hyphae. In the Ascoboleae the larger turbinulate apothecia are 5–8 mm. wide, *e.g. Ascobolus viridis, A. stercorarius*, and the smallest are less than 0·5 mm. wide, *e.g. A. Winteri, Sphaeridiobolus hyperboreus, Saccobolus depauperatus, Dasyobolus immersus*. In the Pseud-Ascoboleae the angiocarpic forms of *Ascophanus, e.g.*

A. carneus, may commence the series, which passes by reduction of the hymenium through *Rhyparobius* to the cleistocarp of *Thelebolus*, deprived even of ascogenous hyphae. *T. stercoreus* presents the limiting case of a juvenescent sporophytic system in an angiocarpic apothecium; the system is content in its inception. Likewise the immarginate apothecium varies from 2 to 3 mm. in *Pyronema* to 0·2 mm. in *Ascodesmis*, and involves a reduction in both systems of hyphae. The three genera *Pyronema*, *Ascodesmis* and *Zukalina* are classed by Boudier as Immarginatae in opposition to all other operculate genera, classed as Marginatae, but if the immarginate apothecium is merely a special case of the general phenomenon of devolution and no more remarkable than the turbinulate, which has no place in Boudier's system, a classificatory value of major importance which the morphological distinction may seem to possess straightway disappears. *Pyronema* and *Zukalina* may be related to *Ascophanus*, and *Ascodesmis* to the Ascoboleae, cf. *Sphaeridiobolus* with similar spore characters, for the apothecium of *Ascodesmis* is so simple that it may be juvenescent on any line of development.

The morphological series in the Clavuleae can be read also by the light of the postulate that all monaxial ascocarps are derivative from the stipitate apothecium. The capitate form in the Leotiaceae is the result of reduction of marginal growth and increase of intercalary hymenial growth; in a sense it is the result of juvenescence of the apothecium on a stalk. The clavate form in the Geoglossaceae may thus be considered the final term with no marginal growth; it corresponds to the primary shaft, or axis, of the stipitate apothecium, over the distal part of which the hymenium is formed. And just as the smaller sessile apothecia may be interpreted as juvenile forms of the larger ones, so may the smaller forms of Clavuleae, 0·5–1 cm. high, be related to the larger, 5–8 cm. high.

Now it seems to me that the ascocarps of *Gyromitra*, *Physomitra*, *Mitrophora* and *Morchella* in the Operculeae can be derived in like manner from the stipitate apothecium. In the extreme forms of the section Adnatae of *Morchella* there is no marginal growth and the intercalary growth of the hymenium is regulated by definite lines of excrescent hyphae. The upper palisade layer of the primordium which produces the hymenium must pass in development through a discoid stage, but the cessation of upgrowth must be localised and proceed centrifugally from numerous small areas by which means the disc becomes alveolate: the margins of the alveoli are sterile and formed of clavate hyphal ends like the margin of a mature apothecium. A morphological series can be traced from the

stipitate apothecium in this way: a form with smooth hymenium but strongly reflexed apothecium, as the first expression of increased intercalary growth, *e.g. Verpa*; a similar form with slight convolution of the hymenium, *e.g. Ptychoverpa*; a capitate form with bullate "head" and reflexed "limb" as the result of extensive intercalary growth and reduced marginal growth, *e.g. Physomitra, Gyromitra*; a similar form with alveolate hymenium, expressing regular intercalary growth, *e.g. Mitrophora*; a similar form with rudimentary reflexed limb, expressing extreme reduction of marginal growth, *e.g.* the section Distantes of *Morchella*; and finally the form of the section Adnatae with no marginal growth, and the hymenium and cortex of the stem apparently confluent. Further intercalary growth makes the secondary fertile convolutions in the alveoli in the section Distantes. The fertile region in *Morchella* may thus result from the complication of a terminal apothecium and need not be considered compound and equivalent to several confluent apothecia, as suggested by Boudier.

Two separate, though related, series of Operculeae with this modification of the stipitate apothecium can be distinguished. The series agree in the possession of a brown pigment in the paraphyses and in the absence of an amyloid substance in the ascus wall, but in one the spores are guttate, commonly triguttate, and in the other they are eguttate. In the series with eguttate spores may be placed *Morchella, Mitrophora, Ptychoverpa, Verpa* and *Disciotis* which has substipitate or sessile cupular apothecia which may even be lenticular, *e.g. D. ferruginascens.* In the other series may be placed *Gyromitra, Physomitra,* and *Discina* which corresponds to *Disciotis*; an ordinary stipitate apothecium does not occur. The series shows not only the complication of the apothecium, but the degeneration of the ascocarp into the sessile form. *Discina* and *Disciotis* have been widely separated from the other genera in all classifications, but the resemblance between *Discina ancilis* and *Gyromitra gigas* is as great as that between *Galactinia proteana* and its variety *sparassoides,* and moreover in several species of both genera the hymenium tends to become folded and reticulate by intercalary growth. The connection between *Disciotis* and the other genera is not so obvious, but follows from the principle of the classificatory value of hymenial characters and the hypothesis of devolution of the ascocarp proposed in this paper. The two series may be related as subseries with guttate and eguttate spores similar to *Galactinia–Aleuria* in the Aleurieae and *Humaria–Coprobia* and *Ciliaria–Cheilymenia* in the Humariaceae.

But the hypothesis does not rest only on morphological evidence.

The mechanism of the ascocarp.

The function of the ascocarp is the formation and dispersal of wind-borne spores, with a minimum rate, under varying degrees of desiccation in subaerial environment. Generally, so far as is known, the ascocarp is without special means of resisting desiccation, and the quicker the function is performed the less the risk of premature stoppage through loss of water and other adversities, *e.g.* unsuitable temperature, attacks of animals and moulds, or growth of bacteria in the residual epiplasm on the hymenium, according to Falck (16), all of which have their value, but are difficult to estimate in the absence of exact observation: slugs, grubs, nematodes, etc., are very partial to apothecia. Hence to appreciate the mechanism of the ascocarp, a knowledge of the period of development or inactivity, of the period of sporing or activity, and of the rate of sporing is required, but data on these points are few and casual. The following are some observations made on the longevity of the apothecium which have some bearing on the points, but it should be noted that the period of sporing refers only to mature apothecia in which marginal growth has ceased, and does not necessarily signify the whole period of activity. The fruit bodies were kept on the original substratum in a moist atmosphere in a room where the temperature unavoidably varied from 14 to 22° C. during the observations: they spored incessantly day and night.

Table I.

Species	Width of apothecium (mm.) When sporing begins	Width of apothecium (mm.) At maturity	Period of sporing: At maturity (days)
Rhizina inflata ...	*ca.* 20	80–100	40–50
Peziza aurantia ...	12–20	40–60	*ca.* 40
Galactinia proteana ...	10–15	30–40	35–46
Galactinia saniosa ...	8–10	12–15	18–24
Ciliaria asperior ...	—	5–6	9–13
Pulvinula constellatio...	1–2	4–5	12–15
Anthracobia maurilabra	0·5–1	3–4	10–21
Coprobia granulata ...	1·5	3	9–12

The following data (Table II) on the period of development, from the inception of the apothecium to the beginning of sporing, have been collected from other writers.

I also found that the apothecia of *Anthracobia maurilabra* developed from 0·5 mm. wide to their mature width in 8–10 days, at *ca.* 18° C., which thus extends the period of activity in this species to 3–4 weeks. Furthermore it was found that the large cupular apothecia of *Galactinia succosa*, *Aleuria vesiculosa* and *A. repanda* do not begin to spore till they are of such a size

that the disc, if flattened out, would be 2–3 cm. wide: and so late a commencement of activity is probably general in cupular forms.

Table II.

Species	Period of development (days)	Width of mature apothecium (mm.)	Authority
Ascobolus carbonarius	*ca.* 21	4–5	Dodge(13)
Trichophaea abundans	*ca.* 10	1–3	Dodge(14)
Pyronema confluens	4–6	1–2	Claussen(7) Harper(17) Seaver(23)
Ascobolus glaber	6–7	0·5–1	Dangeard(12)
Ascodesmis nigricans	2–3	0·2	Claussen(6) Dangeard(12)
Thelebolus stercoreus	*ca.* 14	0·2	Ramlow(19)

If the period of development in apothecia, 0·5–1 mm. wide, is roughly a week, and in apothecia, 5 mm. wide, roughly two to three weeks, it cannot be less than a month in cupular forms, which is extraordinary for an exposed and unprotected fruit body. The significance of these facts is obvious; the smaller apothecia may perform their function while the larger ones are still developing. Moreover, if the apothecia are destroyed prematurely, the loss will be greater in the larger forms, because it is very doubtful if the food reserves could be transported back to the mycelium after the death of the medullary hyphae. Hence in small apothecia both the risk and the magnitude of destruction are diminished. And incidentally it may be noticed that in temperate regions the suitable periods of fructification, March–May and August–November, are not excessive for the functioning of large apothecia which require one month for development and two months for sporing: probably a large number are destroyed prematurely with considerable loss to the mycelium.

Other things being equal, the smaller the apothecium the lower will the spore output be, but it does not follow that the output per fungus is affected by the smallness of the fruit body. It is not the output per apothecium but the output per mycelium, that is "asci per unit hymenial area × total hymenial area per mycelium," which is of importance, but in either case there are no data. However, from general observation, smallness of the ascocarp is compensated by increased production. The small apothecia of *Ascobolus*, *Ascophanus*, *Rhyparobius*, etc., on dung, and of *Pyronema*, *Anthracobia*, etc., on burnt ground, for instance, are normally closely packed in crusts of several square inches, and with unusually favourable conditions there may be outbursts of such apothecia. Massee(18) says that he has seen the apothecia of *Melastiza miniata* "covering the sides of a damp

path and extending for more than a hundred yards...as a crimson streak...," and in August, 1928, I found three or four acres of burnt ground on Bagshot Heath, in Surrey, covered every few inches with colonies of the apothecia of *Anthracobia maurilabra*; there were literally millions of apothecia, and they were all destroyed by the drought in the following September. The aggregate hymenium of such crusts is limited to one plane and is therefore less efficient than the reticulum produced by the aggregation of a smaller number of cupular apothecia, but against this fact must be weighed the economy in sterile tissue in the smaller forms. The point leads to another biological significance of smallness of the fruit body.

The quantity of material required to make an apothecium can be taken as proportional to its volume or, simply, to the volume of the hymenium. The shape of the hymenium is cylindrical and, as the height is roughly the same, *ca.* 200 μ, in all forms the quantity of material is proportional to the diameter of the disc. Comparing an apothecium 5 cm. wide with one 1 mm. wide the quantities are as 2500 : 1; the ratio is certainly too low on account of the disproportionate increase of sterile tissue in larger forms. The fact has a twofold significance because it means that small apothecia can be produced after a shorter period of vegetation in ephemeral habitats, and also in places where the food supply is absolutely too poor to allow of the production of large forms. The possession of small ascocarps by coprophytes, bryophilous parasites, and the innumerable Inoperculeae which live on dead leaves, stems and other herbaceous relics is thus easily explained: the production of a cupular apothecium by a bryophilous parasite is perhaps a nutritional impossibility. It is just those forms of ascocarp which are considered reduced and juvenile which are characteristic of specialised habitats where smallness and quick returns are in demand. The writer has collected the following data on the time interval between spore germination and the commencement of spore discharge in such juvenile forms: twenty days in *Trichophaea abundans* (Dodge), seven to eight days in *Ascobolus glaber* (Dangeard), eight days in *Pyronema confluens* on artificial media (Claussen), and ten days on sterilised soil (Seaver), and four to five days in *Ascodesmis nigricans* (Dangeard). These species are ephemeral, unlike those of *Morchella*, *Geoglossum* or *Peziza*, for example, which fructify in temperate regions at most only once a year, in the spring or in the autumn.

The biological value of small fruit bodies is so marked that some explanation is required of the existence of helvelloid, morchelloid and clavate forms of ascocarp. There are five relevant properties and probably more will be found when they are

better known. Firstly, the mechanism of the ascocarp is very different from that of the sessile apothecium. Owing to indirect development, the fruit body develops as a primordium more or less immersed in the substratum, and thus the risk of desiccation during the lengthy period of inactivity is minimised. Towards the end of development the hymenium is projected by the comparatively speedy elongation of the stem for spore discharge. But, from Falck's observations on *Helvella*, *Gyromitra* and *Morchella*, sporing does not begin until the stem is fully elongate, and lasts only for a few days. *Ptychoverpa bohemica* he calls a "one-day fungus" and implies that sporing is finished in a few hours. The short period of activity agrees with the exposure of the hymenium, but it must limit the spore output by preventing the continued intercalation of asci. Secondly the elevation of the apothecium on a stem allows of increase in area of the hymenium by convolution, reticulation and recurvature of the sides of the apothecium, without interfering with free dispersal of the spores, to an extent that is impossible in sessile forms (and it is just the stipitate forms which possess complications of the hymenium). A high rate of sporing can thus be maintained, despite the short period of activity. Thirdly, marginal growth is a slow process, and the loss of it in morchelloid and clavate forms probably contributes to their efficiency. Fourthly, intercalary growth of the hymenium is more economical in sterile tissue than marginal growth, and the exchange will also contribute to the efficiency of these forms. And fifthly, species with large ascocarps are characteristically forest dwellers, growing in humus and, may be, as mycorrhiza, under conditions which allow lengthy periods of vegetation and lessen the risk of premature destruction of the ascocarp; they do not occur in the more specialised habitats. Falck considers the stem of great assistance in the dispersal of spores by giving them a start above the substratum, but even so, such mechanism recedes before that of *Dasyobolus immersus*, described by Buller (5). This fungus prepares hordes of minute turbinulate apothecia beneath the surface of the dung of sundry animals. The large asci begin to mature in the morning, protruding through the surface, and being heliotropic they turn towards the light. And every day for a week or so each apothecium fires off about noon a salvo of half a dozen spore packets with such violence that they fly upward through the surrounding herbage for 25–35 cm.; and they would thus pass well over the top of a fair-sized morel which might be standing near.

Variations of the ascocarp.

Variation in the development of the ascocarp is so common that it attracts little notice. But on inspection the variation is found to be exactly of the kind required by a hypothesis of juvenescence because it is due mainly to the varying extent of the developmental processes. A few examples may be given, though, being so largely a matter of size, one may be found in every specific description. The extent of upgrowth may vary in stipitate apothecia and substipitate, and even sessile forms may occur in the same species, *e.g. Sarcoscypha coccinea*, *Acetabula leucomelas*, *A. vulgaris*. Durand (15) describes extraordinary variation in *Mitrula irregularis* which has normally a clavate ascocarp, but it may be sessile and pulvinate with a minimum amount of upgrowth; the species is aparaphysate and of very obscure construction. The extent of marginal growth may vary considerably in sessile apothecia, producing when extreme the "forma minor." The apothecium of *Peziza aurantia*, one of the most variable, is normally 4–8 cm. wide, but it may mature when only 5–10 mm. wide when it might as well be classed in *Humaria*; the other varieties of this species have already been described (11). The apothecium of *Melastiza miniata* is normally *ca.* 2 cm. wide, but it may mature at *ca.* 5 mm. when it has been described as belonging to another species, *M. Chateri*, according to Boudier. The lenticular apothecia of *Lamprospora dictydiola*, normally 3–5 mm. wide, may be barely 1 mm. wide according to Seaver (22), as I also have found. The turbinulate apothecia of *Ascobolus stercorarius*, normally 3–5 mm. wide, may not exceed 0·5 mm. and yet mature normal asci (11). And, in an unnamed species of *Rhyparobius*, Barker (1) found that the apothecia produced normally in culture about 50 asci, but they were apt to degenerate, owing perhaps to malnutrition, and might produce only a single ascus. Unfortunately Barker did not describe such a form, which must be nearly identical with the normal state of *Thelebolus stercoreus*.

These facts show that the ascocarp can mature precociously and it requires only the insistence of this precocity to produce the different forms in Discomycetes.

Wynnea (= *Midotis* sensu Sacc.).

If the stipitate apothecium is the starting-point of a series of juvenile forms of monaxial ascocarp, may it not itself be a juvenile form of a more elaborate structure? The answer is perhaps supplied by the little-known genus, *Wynnea*, created by Berkeley and Curtis in 1866 (2). The ascocarp of *Wynnea* consists of a thick stem, or trunk, several centimetres long, sub-

divided distally into many short branches from which numerous large auriculate apothecia arise. Saccardo (21) describes about ten species, but whether they are operculate or inoperculate has yet to be learnt; judging from other characters the genus probably contains species belonging to both sections. The species are lignicolous in tropical forests with the exception of *W. americana* which Thaxter has described with a beautiful illustration (24). This species extends as a humus dweller into the forests of North America, where the action of the seasons, by limiting the periods of vegetation and fructification, may have caused the less elaborate ascocarp and the development of a special perennating organ. The main stem grows from a large sclerotium, which is buried in the humus, and bears about twenty-five apothecia, which may measure as much as 13 × 6 cm. Cooke has illustrated two other species, *W. gigantea* and *W. macrotis* (8); the apothecia are much more numerous and are said to proliferate from the margin, but Thaxter has questioned the accuracy of Cooke's drawings and descriptions. Bresadola describes a similar proliferation in *Midotis Heinricherii* (4).

But biologically, as well as morphologically, the ascocarp of *Wynnea* may be deemed the most archaic of living Discomycetes. The periods of development and spore discharge must be longer than in any other ascocarp, as it is the largest and most elaborate and without indication of indirect development. Moreover, the species of *Wynnea* live in just those parts of subaerial environment where vegetation and the growth of a fungal fruit body are least open to interruption.

Now, at least three conclusions may be drawn from the application of the process of juvenescence to such a multaxial soma. Firstly, the stipitate apothecium can be interpreted as an extreme juvenile form limited to the main stem and first apothecium. Ascocarps with two or three apothecia borne on a common stem must have existed therefore, though apparently extinct nowadays unless as an occasional variation, for instance, in *Sclerotinia*. This genus may also be primitive in respect of the large amount of marginal growth and the direct development of the stem. Secondly the production of numerous apothecia may be retained while the stem disappears, cf. the sessile apothecium, in which case a group of apothecia arising from a common base results, *e.g. Otidea cochleata*. A reduction of the main stem and branches can be seen in *W. americana* and a final vestige of the multaxial soma may be recognisable in the clustered habit which is so common with cupular forms. Thirdly it is possible that the main stem and branches may be retained while marginal growth disappears, giving a multaxial soma with clavate fertile parts, of which the ascocarp of the

Geoglossaceae is but a juvenile form limited to the main axis. In any case the origin of the factors of construction of the stipitate apothecium can be explained because upgrowth, marginal and intercalary growth are inherited from a more elaborate state. Hence the crux of the hypothesis is the origin of the multaxial soma, which will be considered in another paper.

Number of forms of ascocarp.

The suitability of any kind of organism to its environment is shown by the variety of the kind and may be roughly measured by the number of its species. Moreover, such a measure taken at the present time must represent at least an approximation to the outcome of evolution.

If small fruit bodies are best suited to subaerial environment, then species of Discomycete with small ascocarps should be most numerous. The following figures taken from Saccardo's *Sylloge* show that this is the case. It should be mentioned that Saccardo's classification is artificial, and the classes and genera, being defined chiefly by the form of the ascocarp, lend themselves to such enumeration. The Helvelleae comprise all stipitate forms, and the Pezizeae all sessile forms, whether they are operculate or inoperculate. The Ascoboleae have been included, however, for obvious reasons in the Pezizeae, and *Acetabula* and *Macropodia* have been reckoned with the Helvelleae. There are about ten species of *Wynnea*, about twenty genera and three hundred species of Helvelleae and one hundred genera and three thousand three hundred species of Pezizeae. That is, roughly, 0·3 per cent. of living Discomycetes are multaxial, 8·3 per cent. monaxial and stipitate, and 91·4 per cent. monaxial and sessile. But no account has been taken of Dermateae, Bulgarieae, Sticteae, etc., which would swell the ranks of sessile ascocarp enormously, and magnify the differences between the kinds. The largest genera are *Helotium* (280), *Humaria* and *Dasyscypha* (220), and *Mollisia* (210), all of which include only species with small apothecia. They are followed by *Peziza* and *Phialea* (160), *Pezizella* (140), *Trichopeziza* (120), *Pyrenopeziza* (100), *Belonidium*, *Sclerotinia* and *Tapesia* (80), *Ascobolus* and *Pseudohelotium* (70), *Ascophanus*, *Erinella*, *Geopyxis* and *Lachnella* (60), which may be compared with *Morchella*, *Gyromitra*, *Helvella*, *Discina*, *Sarcoscypha*, *Mitrula* and *Geoglossum*, each with about forty species. *Lachnea* with one hundred and eighty species includes both cupular and sessile forms of pilose apothecium.

The facts accord with the hypothesis of degeneration of the ascocarp.

Summary.

A hypothesis is proposed of the degeneration of the ascocarp by juvenescence from the multaxial form, represented nowadays in the genus *Wynnea*. The stipitate apothecium is considered to be a juvenile form limited to the main stem and first apothecium of the multaxial form. The clavate ascocarp of Geoglossaceae is considered homologous with the main stem, but with indirect development. Capitate, helvelloid and morchelloid forms of ascocarp are considered variations of the stipitate apothecium produced by reduction of marginal growth, increase of intercalary growth and indirect development. Juvenescence of the stipitate apothecium gives the variety of sessile forms. The hypothesis rests on the following facts:

That the mature forms of ascocarp constitute a developmental series, the entirety being embodied in the development of the most complex.

That degeneration is consonant with the biological value of smallness and precocity of the fruit body in subaerial environment.

That there is even the requisite variation in the development of the ascocarp within specific limits at the present time.

That small forms of ascocarp are characteristic of specialised habitats and the simplest are coprophytes, *i.e.* Ascobolaceae.

That the construction of such simple forms corresponds to a juvenile stage in the development of a more complex ascocarp in allied species or genera, and there is no simple form known which cannot be so related.

That 91 per cent. of modern Discomycetes have sessile apothecia, and the smaller forms preponderate.

That the opposite case of *Wynnea*, 0·3 per cent. of modern Discomycetes, is explicable as vestigial in the least specialised stations of subaerial environment.

That degeneration of the ascocarp is polyphyletic, and the evolution of Discomycetes conforms therefore in this respect with the universal principle of homoplasy.

The first three facts clearly signify an evolutionary process, namely, results in accordance with an observed variation and a selective force.

The bearing of the hypothesis on the classification of Discomycetes is briefly considered.

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BRITISH XYLARIACEAE*.

By Julian H. Miller.

(With Plates VI and VII.)

This investigation is based on herbarium specimens collected by Mr E. W. Mason and others over a period of several years, and is confined to the genera *Hypoxylon*, *Daldinia*, and *Camarops*.

* The writer wishes to express his appreciation to Mr E. W. Mason of the Imperial Bureau of Mycology, Kew, for his kindness in making available specimens from his herbarium. He is also indebted to Miss E. M. Wakefield of the Royal Botanic Gardens, Kew, Professor J. A. Nannfeldt of the Botanic Institution at Upsala, and Professor W. J. Lütjeharms of the 'Rijks Herbarium at Leiden, for comparing specimens with types, and to Dr F. J. Seaver of the New York Botanic Garden and Dr Roland Thaxter of Harvard for the loan of specimens.

The first two genera are particularly well represented, but there is only one specimen of *Camarops*, which is apparently rare in England. The large number of specimens, as well as the wide range of territory over which the collecting was done, should make this paper inclusive of most of the English species.

The limitations of the genera will be those set forth by the writer (9). *Hypoxylon* will be restricted to effused to globose forms, which are not stipitate and not conspicuously zonate. This genus will include species previously placed in *Nummularia* and *Ustulina*. *Daldinia* will be limited to pulvinate to globose forms, sometimes stipitate, which are dark inside, and in which the stroma is strikingly zonate. *Camarops* will include *Hypoxylon*-like forms with elongate, cylindric perithecia, with short necks, arranged in parallel series.

Since the types of most of the species incorporated in this investigation are in European herbaria, it has been impossible for the writer to see all of them. However, thanks to the kindness of the mycologists at these institutions, comparisons have been made with most of the types.

In this group of fungi certain characters have been used extensively in taxonomic works that have no particular significance because of their extreme variability. The limits of these characters, as well as those that are fairly constant, should be understood before determinations are attempted.

The sterile fungous tissue in which the perithecia develop is called the stroma. The outer layer is the ectostroma and the tissue directly under this in which the perithecia are initiated is the entostroma. In most species the size of the stroma is dependent entirely on the character of the substratum. Forms that are pulvinate or semi-globose when erumpent from firm bark are usually thin and widely effused on hard decorticated wood. The texture of the stroma is fairly constant, being hard and carbonaceous, leathery or woody. When young, all species are fleshy-leathery. The colour varies with age. The so-called coloured species are black when old, and the black forms are coloured when very young; so it is impossible to separate species or groups of species on colour characters, or on those pertaining to stromal form.

The perithecia develop in the upper part of the entostroma just under the ectostroma and penetrate the latter by a short ostiolar neck. This is true for the genera described in this paper. In the genus *Anthostoma* the perithecia are found at the base of the entostroma and the necks are therefore rather long. The transitions between this condition and that found in *Hypoxylon* form a perfect series, and we have such species as *Hypoxylon discretum* (Schwein.) Berk., *H. ohiense* Ell. & Everh. and *H. lu-*

teum (Alb. & Schwein.) Fr., which could be placed in either genus. The position of the perithecia varies from a single layer at the base of the stroma to an irregularly many-layered condition. *Bolinia tubulina* (Alb. & Schwein.) Sacc. also falls in this intermediate group. The writer thinks it best to leave these species in *Hypoxylon* rather than create a new genus, or assign them to *Anthostoma*. If one continues to create new genera for intermediate forms such splitting would end with each species becoming a separate genus.

The size of the perithecia is dependent on the extent to which they are crowded in the stroma, and except within very wide limits has no diagnostic value.

The perithecial neck penetrates entirely through the ectostroma, forming a papillate ostiolum as in *H. serpens* Fr., or it may not project beyond the surface as in *H. rubiginosum* (Pers.) Fr. producing an umbilicate ostiolum.

The asci are borne in fascicles and are attached at different points on a main hypha, maturing successively, so that in a mount one rarely finds all the spores at the same stage of maturity, which accounts for differences in spore measurements within the same perithecium. When specimens are placed in a herbarium the spore development ceases, and so if a type specimen is immature when collected the spores will always be light coloured with distinct oil drops, and will not have the characteristic shape or size. It will always be a source of confusion in making comparisons. However, the spore measurements are the most constant character, provided only mature spores are measured.

The spores are often uniseriate in the ascus, but usually they are diagonally overlapping. Measurements taken of the ascal spore part would of course be much shorter in the latter condition than in the former.

I. ***Hypoxylon*** Fr. *Summa Veg. Scand.* (1849), p. 383.
Hypoxylon Bull. pro parte. *Champ.* I (1791), p. 168.
Sphaeria pro parte. Fr. *Syst. Myc.* II (1823), pp. 331–368.
Hypoxylon Fr. emend. Mill. *Myc.* XX (1928), p. 309.

Stroma globose, pulvinate or effused, erumpent, fleshy when young, leathery, woody or carbonaceous when mature; perithecia several to many in the stromata; paraphyses numerous, thread-like, early gelatinising; asci cylindrical, arranged on sides and base of perithecia; ascospores continuous, elliptical, brown to black, with an elongate, hyaline depression, uniseriate or diagonal in the ascus.

Conidial layer formed first on exposed ectostroma, later

developing on any part of old stromata in favourable weather; conidiophores branched, hyphomycetous, hyaline to greenish brown; conidia minute, continuous, borne apically, one to many, becoming lateral by the sympodial growth of the hypha.

The generic name *Hypoxylon* was created in 1791 by Bulliard, but he placed in this only five species which Fries later recognised as valid. Fries in 1849 brought together for the first time clearly related forms under this name, and so should be credited with the genus.

No type was designated by either Bulliard or Fries, but the writer thinks that the five species which Fries accepted from Bulliard should be considered as typical. They are *H. ustulatum*, *H. nummularium*, *H. coccineum*, *H. granulosum* (*H. multiforme* Fr.), and *H. glomeratum* (*H. fuscum* Fr.).

In the following key *H. luteum* is separated off by its many-layered perithecial character, and the main group is divided by the character of the perithecial neck. This ostiolar character can be plainly seen with a hand lens. The further divisions based on the dimensions of spores will operate only for mature ones. The secondary divisions are similar to Nitschke's sections *Eu-hypoxylon* and *Epixylon* (11); in the former the ostiola are umbilicate and in the latter papillate, but Nitschke also uses separations based on the shape of the stroma, which are useless considering the variability of that tissue. Nitschke's last section, *Endoxylon*, contains the species *H. semi-immersum* Nits., and is separated by the perithecial stroma being more or less immersed in the substratum. This separation does not appear to be a good one, because the species placed in it are immersed only when the wood is very soft, and that holds true for species in his other sections.

Key to the species of Hypoxylon.

A. Perithecia monostichous

1. Ostiolar necks extruded beyond ectostroma
   a. Ascospores not over 10 μ in length
      Stroma 2–4 mm. in diameter, on *Fagus*
      H. cohaerens
      Stroma pulvinate to widely effused, on *Betula*
      H. multiforme
      Stroma globose to hemispherical, slightly effused, on decorticated wood; on *Fagus*
      H. rutilum
   b. Ascospores over 10 μ in length
      Stroma widely effused. Spores 10–15 μ in length
      H. serpens

Stroma small, 2–4 mm. in diameter. Spores between 15 and 22 μ in length
H. semi-immersum
Stroma widely effused. Spores 27–34 μ in length
H. ustulatum

2. Ostiolar necks not extruded
   a. Ascospores 10–12 μ in length
      Stroma pulvinate on bark to widely effused on decorticated wood *H. rubiginosum*
   b. Ascospores 12–15 μ in length
      Stroma bright red at maturity; on *Fagus*
      H. coccineum
      Stroma purplish brown at maturity; on *Corylus*, *Alnus* *H. fuscum*
   c. Ascospores 16–20 μ in length
      Stroma clay-coloured at maturity
      H. argillaceum

B. Perithecia polystichous *H. luteum*

1. ***Hypoxylon cohaerens*** (Pers.) Fr. *Summa Veg. Scand.* (1849), p. 384.
   Sphaeria cohaerens Pers. *Syn. Meth. F.* (1801), p. 11.
   S. cohaerens Fr. *Syst. Myc.* II (1823), p. 333.
   S. turbinulatum Schwein. *Syn. N. Am. F.* no. 1204 (1832).
   Hypoxylon Bagnisii Sacc. *Syll.* I (1882), p. 357.
   H. turbinulatum Ell. & Everh. *N. Am. Pyr.* (1892), p. 636.
   H. atrorufum Ell. & Everh. *N. Am. Pyr.* (1892), p. 742.

   Type: Fries, Scler. Suec. no. 43.

   (Pl. VI, fig. 5; Pl. VII, fig. 1.)

Stroma erumpent from bark or on decorticated wood, usually closely gregarious to connate, hemispherical to turbinate and constricted below, 2–4 mm. in diameter and 1–2 mm. thick; young stroma light brown, varying to a deep mahogany-brown, to black at maturity; perithecia 6–50 in a stroma, variable in size, with papillate ostiola; asci cylindrical, tapering to a long stalk, 60–80 × 7 μ (p. sp.), and stalk 65–85 μ; ascospores dark brown, inequilaterally elliptical at maturity, 9–11 × 4–5 μ (most spores 10 × 4 μ); conidiophores forming an uniform layer over the stroma, branched, pale brown appearing hyaline under the microscope; conidia hyaline, minute, 3–5 × 2·5–4 μ.

Common on *Fagus* in both Europe and America. Doubtfully reported on other hosts.

This species often occurs with *H. coccineum* Bull., from which it differs in its smaller turbinate stromata as well as in its smaller spores. It might be confused with some forms of *H. multiforme* Fr.,

but the irregular stroma of the latter and the differences in host should separate them.

Material examined.

Fr. Scler. Suec. no. 43. (Botaniska Institutionen, Upsala. Compared by Nannfeldt.)

Pers. spec. no. 910.270–92. (Under *S. cohaerens* Pers., in 'Rijks Herbarium, at Leiden. Compared by Lütjeharms.)

Moug. et Nestl. Stirp. Vog.-Rhen. no. 764. (At Cornell.)

Roum. Fungi Gall. no. 462. (At Cornell.)

Mason Herb. no. 48 New Forest; no. 49 Burnham Beeches; nos. 59, 60 Norbury Park; nos. 61, 62 Boxhill.

2. ***Hypoxylon multiforme*** Fr. *Summa Veg. Scand.* (1849), p. 384.

Sphaeria multiforme Fr. *Syst. Myc.* II (1823), p. 334.
Hypoxylon granulosum Bull. *Champ.* I (1791), p. 176, tab. 487, fig. 2.
? *Sphaeria rubiformis* Pers. *Syn. Meth. F.* (1801), p. 9.
? *S. granulosa* Pers. *Syn. Meth. F.* (1801), p. 11.
? *S. crustacea* Sow. *Eng. Fung.* I (1809), T. 372, fig. 11.
S. peltata DC. *Flor. Franc.* II (1815), p. 287.
S. atropurpurea Fr. *Syst. Myc.* II (1823), p. 340.
S. transversa Schwein. *Syn. N. Am. F.* no. 1180 (1832).
Hypoxylon atropurpureum Fr. *Summ. Veg. Scand.* (1849), p. 384.
H. crustaceum Nits. *Pyr. Germ.* (1867), p. 49.
H. transversum Sacc. *Syll.* I. (1882), no. 1505.

Type: Fries, Scler. Suec. no. 44.

(Pl. VI, fig. 4; Pl. VII, fig. 2.)

Stroma transversely erumpent from bark, or widely effused on decorticated wood; when on bark 5–20 × 3–10 mm. and 3–7 mm. thick, the shape and size being entirely dependent on the substratum; stroma when young leathery-woody, reddish brown passing into dark brown and at maturity black and carbonaceous; perithecia distinctly prominent, large, with papillate ostiola; asci cylindrical with tapering stalks, 55–75 μ (p. sp.), stalk 60–80 μ in length; ascospores inequilaterally elliptical at maturity, dark brown, 9–11 × $3\frac{1}{2}$–5 μ (most spores 10 × 4 μ); conidial layer variable in colour, usually a dirty yellow; conidia hyaline, minute, 5 × 3 μ.

This species is widely distributed, being common throughout the world on species of *Betula*. It occurs very rarely on other hosts.

When mature it is easily distinguishable from *H. cohaerens* by its irregular stroma, as pointed out above. The flat effused form has often been a source of confusion. Fries (4) named this stage *Sphaeria atropurpurea* and Nitschke (11) continued the error. The specimen in Moug. et Nestl. Stirp. Crypt. Vog.-Rhen. no. 765 at Upsala labelled *S. vogesiaca* Pers. and *S. atropurpurea* in the index, contains three pieces, one is *Hypoxylon multiforme*, and the other two are *H. vogesiacum* (Pers.) Sacc. The Fries specimen, no. 75 under *Sphaeria atropurpurea*, at Upsala is fully equal to *Hypoxylon multiforme* according to Nannfeldt (in litt.). This same young reddish form of *H. multiforme* may be confused with *H. rubiginosum* (Pers.) Fr., but the papillate ostiola in the former and not in the latter will distinguish it.

Fries (4), as well as many other mycologists, consider *Sphaeria granulosa* Pers. as a synonym of *Hypoxylon multiforme*, but according to Lütjeharms (in litt.) there are only two specimens under that name in the Persoon Herbarium. One, no. 910.267–362, has noted on it by Persoon—"*Sph. granulosa* Syn. fun. p. 11? *Sph. multiformis* B Fr." The other, no. 910.267–365, is labelled by Persoon "*Sph. granulosa*? var.?" Neither specimen conforms to *H. multiforme* Fr., as both have umbilicate ostiola. It is thus very doubtful just what Persoon considered *Sphaeria granulosa*.

Sphaeria rubiformis Pers. has also been placed in this synonymy, but with doubtful propriety. According to Lütjeharms the three specimens, 910.269–426, 910.269–437, 910.269–438, have "*Sph. rubiformis*?" written on them by Persoon. These fully equal *Hypoxylon multiforme* Fr., but stress must be laid on the fact that Persoon questioned their identity with *Sphaeria rubiformis* Pers.

Material examined.

Fr. Scler. Suec. no. 44. (Botaniska Institutionen, Upsala. Compared by Nannfeldt.)

Fr. Scler. Suec. no. 75. (Under *Sph. atropurpurea*, at Upsala. Compared by Nannfeldt.)

Pers. spec. no. 910.269–426. (In 'Rijks Herb., Leiden. Compared by Lütjeharms.)

Pers. spec. no. 910.269–437. (In 'Rijks Herb., Leiden. Compared by Lütjeharms.)

Pers. spec. no. 910.269–438. (In 'Rijks Herb., Leiden. Compared by Lütjeharms.)

Lütje. spec. no. 929.213–14. (In Univ. of Georgia Herb.)

F.C. nos. 125, 242. (At Cornell.)

Ell. & Everh. N.A.F. no. 575. (At Cornell.)

Rabh. F.E. no. 2433. (Under *Hyp. crustaceum*, at Cornell.)

Mason Herb. nos. 1, 3, 4 Aviemore; no. 6 New Forest; no. 8 Rickmansworth; no. 9 Ashtead Downs; nos. 7, 10 Mickleham; nos. 11, 12 Arundel; no. 50 Westcott.

3. ***Hypoxylon rutilum*** Tul. *Sel. Fung. Carp.* II (1863), p. 38.
H. coccineum Bull. var. *microcarpum* Biss. Sacc. *Syll.* IX (1891), p. 545.
H. pulcherrimum v. Höhn. in *Ann. Myc.* III (1909), p. 186.
H. miniatum Cke. in *Grev.* VII (1879), p. 80.
(Pl. VI, fig. 6; Pl. VII, fig. 3.)

Stroma erumpent, hemispherical, on bark, 2–3 mm. in diameter and 1–2 mm. thick; on decorticated wood irregularly effused, 3–10 mm. in diameter and 1–1½ mm. thick; young stroma light reddish brown, at maturity a dark shade of red, and very old specimens almost black; perithecia very small and closely packed, with minute papilliform ostiola necks; asci cylindrical and tapering, 50–60 × 5 μ (p. sp.) with stalk 50–60 μ in length; ascospores at maturity inequilaterally elliptical, 7–10 × 3·3–4 μ. No conidia have been observed.

Chiefly on *Fagus*, but reported on other hosts. Probably limited to Europe, as the writer has not seen this form among American specimens.

This species is apt to be confused with *H. coccineum* Bull., as it occurs on the same host, and in the young condition has very much the same shade of red. The smaller ascospores and the papillate ostiola of *H. rutilum* will separate it. The effused state can be distinguished from *H. rubiginosum* by the same ostiolar character.

The specimen, Rehm Ascom. fasc. 52, no. 2037, labelled *H. rutilum*, is *H. rubiginosum*.

Material examined.

Mason Herb. no. 54 New Forest; no. 55 Minstead; no. 56 Arundel; no. 104 Llanbedr.

4. ***Hypoxylon serpens*** (Pers.) Fr. *Summa Veg. Scand.* (1849), p. 384.
Sphaeria serpens Pers. *Syn. Meth. F.* (1801), p. 20.
S. serpens Fr. *Syst. Myc.* II (1823), p. 341.
? *S. unita* Fr. *Elench. Fung.* II (1828), p. 67.
Hypoxylon unitum Nits. *Pyr. Germ.* (1867), p. 44.
Type: Fries, Scler. Suec. no. 47.
(Pl. VI, fig. 3; Pl. VII, fig. 4.)

Stroma widely effused, smooth and applanate, or irregularly pulvinate, according to the character of the substratum; on

smooth wood thin with closely packed perithecia, and on rough wood or bark much thicker in very irregular shapes with much larger perithecia; at first a dirty white ectostroma arises, which gradually changes to purplish brown and finally to almost black; asci cylindrical, tapering, 60–85 × 6–8 μ (p. sp.), and stalk 50–75 μ in length; immature ascospores oblong with central oil drops, with age becoming inequilaterally elliptical and almost opaque, 10–15 × 5–7 μ; conidia hyaline, minute, 4–5 × 3 μ.

On decaying wood of various deciduous trees. There seems to be no host specialisation. Common in both Europe and America.

Fries in *Systema Mycologicum*, p. 341, gives Persoon credit for this species, but the only authentic specimens of this species in the 'Rijks Herbarium, according to Lütjeharms, show that Persoon was confused as to its identity. No. 910.269–885 is labelled "*Sph. serpens*" by Persoon and is equal to *S. vogesiaca* Pers. no. 910.269–887 and no. 910.269–713 are both labelled "*Sph. serpens* var." by Persoon and have spores 10–15 μ in length, showing that Persoon confused *S. serpens* with *S. vogesiaca*; but as long as the Mougeot specimen, Stirp. Vog.-Rhen. no. 765, has large spores (20 × 10 μ) and is labelled "*Sphaeria vogesiaca* Pers. in litt.", the writer thinks it logical to consider the smaller spored form as *S. serpens*. This has been the practice of most mycologists since the time of Persoon.

This species is most closely related to *Hypoxylon illitum* (Schwein.) Sacc. and *H. albocinctum* Ell. & Everh. All three begin with a greyish white stroma and are black in old age. Dimensions of the ascospores will separate them.

The Fries specimen at Upsala is different from the writer's concept according to Nannfeldt, but the writer has examined the same Fries number at Harvard and thinks it identical with his material. In that specimen the spores vary from oblong to rather widely inequilaterally elliptical, just as in the English and American forms studied here.

Material examined.

Fr. Scler. Suec. no. 47. (At Harvard.)

Pers. no. 910.269–713. (In 'Rijks Herb., Leiden. Compared by Lütjeharms.)

Pers. no. 910.269–887. (In 'Rijks Herb., Leiden. Compared by Lütjeharms.)

Rav. F. Car. no. 34. (At Cornell.)

Mason Herb. no. 35 Ashridge; nos. 36, 37, 38, 98 Arundel; no. 58 no station; no. 89 Boxhill; no. 90 New Forest; no. 96 Norbury Park; no. 106 Mickleham Woods.

5. ***Hypoxylon semi-immersum*** Nits. *Pyr. Germ.* (1867), p. 50.
(Pl. VI, fig. 7; Pl. VII, fig. 5.)

Stroma on decorticated wood, or erumpent through bark, flat, effused irregularly, composed of connate perithecia covered by a thin ectostroma, with very little entostroma and the perithecia seated partially in the wood; orbicular or elongate, 2–15 × 2–8 mm. and 1–2 mm. thick, or 2–8 connate perithecia linearly arranged; young stroma white to light grey and at maturity black; perithecia large with papillate ostiola; asci cylindrical, 80–110 × 10–12 μ (p. sp.) and stalk 60–70 μ in length; ascospores deep brown at maturity, inequilaterally elliptical with pointed ends, 17–20 × 10–12 μ; conidiophores forming a light grey layer over the ectostroma; conidia hyaline, 5–8 × 3–5 μ.

This species occurs on *Quercus*, *Fagus*, *Ulmus* and probably other hosts, and is found in both Europe and America. Judging by the number of collections it seems to be very rare. The Mason material agrees with collections of the writer in America.

Material examined.

Morgan spec. (At Univ. of Iowa.)
Mason Herb. nos. 57, 91 Llanbedr; nos. 92, 93 Ashtead; no. 94 Arundel; no. 95 Somerset.

6. ***Hypoxylon ustulatum*** Bull. *Champ.* I (1791), p. 176, t. 487, fig. 1.

Sphaeria maxima Hall. *Hist. Stirp. Helv.* III (1768), p. 122.
S. deusta Hoffm. *Veg. Crypt.* I (1787), p. 3, tab. 1, fig. 2.
S. versipellis Tode, *Fung. Meckl. Sel.* fasc. II (1791), p. 55, tab. 17, f. 129.
S. deusta Fr. *Syst. Myc.* II (1823), p. 345.
Hypoxylon deustum Grev. *Scot. Crypt. Fl.* VI (1828), tab. 324, fig. 2.
H. ustulatum Fr. *Summ. Veg. Scand.* (1849), p. 383.
Ustulina vulgaris Tul. *Sel. Fung. Carp.* II (1863), p. 23, tab. 3, figs. 1–6.
U. deusta Petr. in *Ann. Myc.* XIX (1921), p. 279.

Type: Fries, Scler. Suec. no. 261.
(Pl. VI, fig. 1; Pl. VII, fig. 6.)

Stroma indefinite, on rough substratum variously distorted, irregularly effused, following the inequalities of the bark, undulate, repand to subpulvinate, 1½–3 mm. thick; on smooth wood applanate and subzonate and much thinner; the young stroma is greyish white, fleshy-leathery, becoming carbonaceous and black with age, the mature stroma easily separating along

the line of the perithecial bases; perithecia very large with papillate ostiolar necks; asci cylindrical and tapering 190–260 × 10–15 μ (p. sp.), stalk 50–60 μ in length; ascospores elliptical to inequilateral, opaque at maturity, 28–34 × 7–10 μ; conidia hyaline, smooth, narrowly obovate, 5–6·5 × 2–3 μ.

Common on deciduous trees in Europe, America and Asia. One of the Mason specimens is on *Taxus*, but it is more common on Angiosperms.

The writer (9) has transferred this form back to *Hypoxylon*, because it has the fundamental characters of the generic concept.

The use of specific name *ustulatum* is open to question. According to a literal interpretation of the rules of the International Code the name *deusta* should be used as Fries accepts it in *Systema Mycologicum*, but it seems more reasonable to accept Bulliard's name *ustulatum*, as Fries did later in *Summa Vegetabilium Scandinaviae* when he created our present concept of the genus *Hypoxylon*.

Material examined.

Fr. Scler. Suec. no. 261. (At Upsala, under *S. deusta* Hoffm. Compared by Nannfeldt.)

Moug. et Nestl. Stirp. Vog.-Rhen. no. 276. (At Cornell.)

Krieger, Fungi Saxonici nos. 1334, 2372. (At Cornell.)

Baker, Philipp. Fung. no. 1236. (At Univ. of Georgia in part, under *U. macrosperma*.)

Baker, Philipp. Fung. nos. 3516, 1191. (At Univ. of Georgia in part, under *U. zonata*.)

Mason Herb. no. 2 Richmond; nos. 64, 65, 97 Mickleham Woods; no. 66 Arundel.

7. ***Hypoxylon rubiginosum*** (Pers.) Fr. *Summ. Veg. Scand.* (1849), p. 384.

Sphaeria rubiginosa Pers. *Syn. Meth. F.* (1801), p. 11.
S. perforata Schwein. *Syn. Car.* no. 45 (1822).
S. rubiginosa Fr. *Syst. Myc.* II (1823), p. 340.
S. decorticata Schwein. *Syn. N. Am. F.* no. 1179 (1832).
S. fuscopurpurea Schwein. *Syn. N. Am. F.* no. 1209 (1832).
S. Catalpae Schwein. *Syn. N. Am. F.* no. 1214 (1832).
Hypoxylon perforatum Fr. *Summ. Veg. Scand.* (1849), p. 384.
H. luridum Nits. *Pyr. Germ.* (1867), p. 31.
H. purpureum Nits. *Pyr. Germ.* (1867), p. 37.
Diatrype cercidicola Berk. & Curt. in Pk. *25th Rep. N.Y. State Mus.* (1873), p. 101.
Hypoxylon crocopeplum Berk. & Curt. in *Grev.* IV (1875), p. 50.

H. florideum Berk. & Curt. in *Grev.* IV (1875), p. 50.
H. decorticatum Berk. in *Grev.* IV (1875), p. 50.
H. suborbiculare Pk. *30th Rep. N.Y. State Mus.* (1878), p. 63.
Anthostoma cercidicolum Sacc. *Syll.* I (1882), p. 306.
Hypoxylon Catalpae Sacc. *Syll.* I (1882), p. 392.
H. piceum Ell. in *Amer. Nat.* XVII (1883), p. 194.
H. subchlorinum Ell. & Cal. in *Journ. Myc.* IV (1888), p. 86.
H. subluteum Ell. & Everh. *N. Am. Pyr.* (1892), p. 648.
Nummularia lateritia Ell. & Everh. in *Phila. Acad.* (1893), p. 144.
Hypoxylon lianicalum Rehm, *Ascom. Philipp.* IV, in *Leaf. Philipp. Bot.* VII (1913), p. 1942.

Type: Fries, Scler. Suec. no. 142.

(Pl. VI, fig. 11; Pl. VII, fig. 10.)

Stroma pulvinate to effused, indefinite in extent, continuous for several centimetres on decorticated wood, or 1–3 mm. thick when erumpent from bark; young stroma fleshy-leathery, at maturity woody, very old specimens crumbling, never carbonaceous; colour of stroma varying, when young bright brick-red to purplish red to shades of reddish brown, becoming black with extreme age; perithecia variable in size, depending on distance apart in stroma; ostiolar necks umbilicate, often containing a white mycelial growth in the ostiolum; asci cylindrical, tapering to a long stalk, 70–80 × 7 μ (p. sp.) and 65–80 μ for the stalk; ascospores at maturity dark brown, inequilaterally elliptical, 9–12 × 4–6 μ; conidia minute, elliptical, 4–5 × 3 μ.

No host specialisation has been found. This fungus seems to grow equally well on almost all deciduous trees, and is probably the most common species throughout the world.

Pulvinate forms are sometimes confused with *H. coccineum* and *H. fuscum*, but the larger ascospores of those species will separate them from *H. rubiginosum*.

Material examined.

Pers. spec. no. 910.263–1191. (In 'Rijks Herb. at Leiden. Specimen very old and doubtfully this species. Compared by Lütjeharms.)

Fr. Scler. Suec. no. 142. (At Upsala. Compared by Nannfeldt.)

Baker, Philipp. F. no. 1186. (Under *H. lianicalum*, det. Rehm. Part at Univ. Georgia.)

E. & E. N.A.F. 2nd ser. no. 2157. (Under *H. subchlorinum*, at N.Y. Bot. Garden.)

Morgan no. 212. (Under *N. lateritia*, det. Ellis, at Univ. of Iowa.)

Fautrey no. 2616. (Under *H. luridum*, at Univ. of Iowa.)

Rev. F. Am. nos. 654, 741. (At Cornell.)
Rav. no. 1579. (Under *H. florideum*, at Kew. Compared Wakefield.)
Rav. no. 1906. (Under *H. crocopeplum*, at Kew. Compared Wakefield.)
F.C. no. 1647. (Under *H. perforatum*, at Cornell.)
F.C. nos. 2034, 2122. (Under *H. fuscopurpureum*, at Cornell.)
Rick, Fungi Austro-amer. fasc. II, no. 303. (At Univ. of Georgia.)
Mason Herb. nos. 34, 82, 83, 84, 88, 100, 101, 103 Arundel; nos. 52, 53, 79 Norbury Park; no. 71 Lessness; no. 72 Devon; no. 73 Somerset; no. 74 Hereford; no. 75 Boxhill; no. 77 Mickleham Woods; no. 76 Grabhurst; no. 81 Richmond Park; nos. 86, 87 no station.

8. ***Hypoxylon coccineum*** Bull. *Champ.* I (1791), p. 174, tab. 345, fig. 2.

Valsa fragiformis Scop. *Flor. Carn.* ed. 2 (1772), t. 2, p. 399.
Sphaeria rubra Willd. *Flora Berol.* (1787), p. 415.
S. radians Tode, *Fungi Meckl. Sel.* II (1791), p. 29.
S. fragiformis Pers. *Syn. Meth. F.* (1801), p. 9, no. 13.
S. tuberculosa Sow. *Eng. Fung.* III (1809), tab. 374, fig. 8.
S. bicolor DC. *Flor. Franc.* II (1815), p. 286.
S. latentia DC. *Flor. Franc.* IV (1815), p. 137.
S. fragiformis Fr. *Syst. Myc.* II (1823), p. 332, no. 19.
Stromatosphaeria fragiformis Grev. *Scot. Crypt. Fl.* III (1825), tab. 136.
Hypoxylon coccineum Fr. *Summ. Veg. Scand.* (1849), p. 384, no. 11.
H. fragiformis Petr. in *Ann. Myc.* XIX (1921), p. 277.

Type: Fries, Scler. Suec. no. 41.

(Pl. VI, fig. 8; Pl. VII, fig. 7.)

Stroma globose to hemispherical, 2–8 mm. in diameter, solitary or connate, at maturity distinctly roughened by the prominent perithecia; at an early stage the stroma is light salmon-pink, changing to a deep brick-red when mature, and in age turning to a brown-black, the texture varying from fleshy-leathery to woody; asci cylindrical, tapering to a long stalk, spore part 70–85 μ long, with stalk of equal length; ascospores uniseriate, opaque at maturity, inequilaterally elliptical, 11–15 × 5–7 μ; conidial layer some shade of yellow; conidia minute, hyaline, 5 × 3–4 μ.

On decaying limbs of *Fagus*, widespread in both Europe and America. It has been occasionally reported on other deciduous trees.

The conidial growth frequently found in connection with this fungus, which has been called *Institale acariforme* Fr., does not belong to its life-history, and is probably a parasite.

This species is closely related to *H. Howeianum* Pk. and *H. rutilum*. The young stromata are similar in consistency and colour and it seems impossible to separate them except when forms with mature spores are present, the last two having much smaller spores.

Fries in *Systema Mycologicum* used the specific name *fragiformis*, but the writer thinks it preferable to retain *coccineum* because Fries accepted that name in *Summa Vegetabilium Scandinaviae* under the genus *Hypoxylon*.

Material examined.

Fr. Scler. Suec. no. 41. (At Upsala, under *S. fragiformis*. Compared by Nannfeldt.)

Moug. et Nestl. Stirp. Vog.-Rhen. no. 273. (Under *S. fragiformis*, at Cornell.)

Pers. spec. no. 910.267–646. (At Leiden, under *S. fragiformis*. Compared by Lütjeharms.)

Rabh. F.E. nos. 172, 670, 920. (At Cornell.)

Roum. Fung. Gall. nos. *72a*, *72b*. (At Cornell.)

Mason Herb. no. 40 Keswick; no. 41 Cambridge; no. 42 Mickleham; no. 43 Norbury Park; no. 44 no station; nos. 45, 46 Arundel; no. 47 no station.

9. ***Hypoxylon fuscum*** (Pers.) Fr. *Summ. Veg. Scand.* (1849), p. 384.

Sphaeria fusca Pers. *Syn. Meth. F.* (1801), p. 12.
S. fusca Fr. *Syst. Myc.* II (1823), p. 332.
S. fragiformis Hoff. *Veg. Crypt.* I (1787), p. 20.
S. confluens Willd. *Flora Berol.* (1787), p. 416.
S. tuberculosa Bolt. *Fung. Halif.* (1788), p. 123, tab. 123, fig. 1.
S. castorea Tode, *Fung. Meckl. Sel.* II (1791), p. 28.
S. Coryli et *glomerulata* DC. *Fl. Fr.* II (1815), p. 287.

Type: Fries, Scler. Suec. no. 42.

(Pl. VI, fig. 10; Pl. VII, fig. 8.)

Stroma erumpent, superficial, gregarious to solitary, hemispherical or depressed, 2–4 mm. in diameter and 1–3 mm. thick, or effused on decorticated wood, applanate, 1–3 cm. in length and 1 mm. thick; young stroma a purplish shade varying to a brownish purple or light purplish grey in age; perithecia not prominent, ostiola umbilicate; asci cylindrical, spore part 70–80 μ in length, stalk 60–70 μ; ascospores inequilaterally

elliptical, nearly opaque, 12–15 × 5–7 μ; conidia minute, elliptical, 4–5 × 3 μ, hyaline.

On decaying limbs of *Corylus* and *Alnus*, widespread throughout the temperate regions of the world.

This species is sometimes confused with purple shades of *H. rubiginosum*, but the larger spores will distinguish it from the latter. The purple-brown colour will separate it from *H. coccineum*.

Material examined.

Fr. Scler. Suec. no. 42. (At Upsala. Compared by Nannfeldt.)

Pers. specs. 910.267–140, 910.267–658, 910.267–664, 910.267–675, 910.267–745. (At Leiden. Compared by Lütjeharms.)

Moug. et Nestl. Stirp. Vog.-Rhen. no 178. (At Cornell.)

Rabh. F.E. no. 628. (At Cornell.)

Rav. Fl. Am. no. 184. (At Cornell.)

E. & E. N.A.F. no. 678. (At Cornell.)

Mason Herb. nos. 2*a*, 21, 22 New Forest; no. 23 Minstead; no. 24 Dorking; nos. 25, 26, 27, 28 Ashtead; no. 29 Grabhurst; no. 30 Mickleham; nos. 31, 32, 33, 34 Arundel.

10. ***Hypoxylon argillaceum*** (Pers.) Berk. *Outlines of Brit. Fung.* (1860), p. 387.

Sphaeria argillacea Pers. *Syn. Meth. F.* (1801), p. 10.

Type: Persoon specimen no. 911.18–199.

(Pl. VI, fig. 9; Pl. VII, fig. 9.)

Stroma globose to hemispherical, usually solitary, 2–5 mm. in diameter, erumpent from bark or on decorticated wood, roughened by the projecting perithecia, of soft woody texture, ectostroma light clay colour, entostroma black; perithecia medium size, ostiola umbilicate; asci cylindrical and tapering to a stalk, 110–130 × 10–13 μ (p. sp.), stalk 60–80 μ in length; ascospores broad elliptical to subequilateral for mature spores, nearly opaque, 17–20 × 8–10 μ; conidial layer whitish clay colour; conidia ovate, minute, hyaline, 4–5 × 3 μ.

The writer has seen this species only on *Fraxinus*, but it has been reported on other trees. It occurs in both Europe and America, but is not common.

Two species found in North America, *H. regalis* Morg. and *H. Kellermanii* Rehm, are very closely related to *H. argillaceum* if not identical.

Berkeley (1) credits Fries with this species, but the Fries specimens are other forms. There are two specimens so labelled by Fries at Upsala, one equals *H. coccineum* and the other is a *Melogramma* according to Nannfeldt. There is one other specimen named *Sphaeria argillacea* which Fries received from Berkeley,

and this one is equal to *S. argillacea* in the Persoon Herbarium. Berkeley therefore was the first one to transfer *S. argillacea* Pers. to *Hypoxylon*.

Material examined.

Berk. spec. in Herb. Fries. (At Upsala. Compared by Nannfeldt.)

Pers. spec. no. 910.270–516. (In 'Rijks Herb. at Leiden. Compared by Lütjeharms.)

Pers. spec. no. 910.18–199. (In 'Rijks Herb. at Leiden. Compared by Lütjeharms.)

Roum. Fung. Gall. no. 6839. (At Cornell.)

Rabh. F.E. no. 247. (At Cornell.)

Morgan no. 42. (At Univ. of Iowa.)

Mason Herb. no. 70 Hereford.

11. ***Hypoxylon luteum*** (Alb. & Schwein.) Fr. *Summ. Veg. Scand.* (1849), p. 383.

Sphaeria lutea Alb. & Schwein. *Consp. Fung. in Agr. Niskcres.* (1805), p. 10, tab. 1, fig. 1.

S. lutea Fr. *Syst. Myc.* II (1823), p. 347.

Hypoxylon luteum Berk. *Outlines Brit. Fung.* (1860), p. 386.

Nummularia lutea Nits. *Pyr. Germ.* (1867), p. 59.

(Pl. VI, fig. 13; Pl. VII, fig. 11.)

Stroma erumpent, orbicular to oblong, thick with abrupt sides, surface applanate, undulate or slightly concave, of woody texture, not carbonaceous, 2–10 mm. wide by 5–20 mm. long and 1–6 mm. thick; perithecia ovate to angular by compression, attaining the surface by long ostiolar necks, polystichous; asci cylindric-tapering, 30–50 × 5 μ (p. sp.), stalk 20–30 μ in length; ascospores oblong with rounded ends, olivaceous to almost opaque, uniseriate, 5–7 × 3–4 μ.

The Mason specimen is on *Buxus*, but it is also reported on *Salix* and *Betula*.

The specimen of which the above description is made agrees fully with one at Kew which Berkeley recorded in his *Outlines* according to Mason in letter. It also agrees with a very poor specimen at Upsala labelled by Fries, which has no spores.

As pointed out earlier in this paper this species occupies an intermediate position between *Hypoxylon* and *Anthostoma*. The fact that the perithecia have elongate necks and are arranged at various levels in the stroma suggests *Anthostoma*. Shear (15) made *H. Petersii* Berk. & Curt. the basis of a new genus, *Peridoxylon*, on the characters of polystichous perithecia and a membranous covering over the young stroma. Having no definite peridium, *Hypoxylon luteum* could not be placed there.

H. ohiense Ell. & Everh., *H. succenturiatum* (Tode) Fr., and *Bolinia tubulina* (Alb. & Schwein.) Sacc. all have more or less polystichous perithecia and are closely related to *H. luteum*. *H. discretum* (Schwein.) Berk. has perithecia with elongate necks, but arranged at practically the same level. These species have the *Anthostoma* character of perithecia lying in the lower part of the entostroma and long perithecial necks, but they are also composed entirely of fungous tissue as in *Hypoxylon*.

Material examined.

Fries specimen. (At Upsala. Compared by Nannfeldt.)
Mason Herb. no. 14 Norbury Park (coll. J. H. Harvey Bloom).

II. ***Camarops*** Karsten, *Myc. Fenn.* II (1873), p. 53.

Solenoplea Starback, *Ascom. d. I. Regn. Exp.* II; *Bihang t. K. Svenska Vet. Akad. Handlingar*, XXVII (1901), iii, n. 9, p. 13.

Type species: *Hypoxylon polyspermum* Mont.

Stroma erumpent or superficial, variously shaped following the inequalities of the wood, thick, convex, or undulate-concave, at maturity ferruginous black; perithecia monostichous, densely packed, subcylindric to tubuliform, forming a palisade layer oriented under the ectostroma, ostiolar necks very brief; asci cylindric-tapering; ascospores continuous, dark brown, oblong to slightly inequilateral; conidial layer developing on ectostroma; conidia hyaline, continuous, minute.

The genus *Camarops* Karst. (6) was based on the single species *C. hypoxyloides* Karst. In the specific description he says the spores are spuriously septate and two-guttulate, and Lindau (7) and others have accepted septate spores for this genus to separate it from other members of the Xylariaceae. Rehm (16) in a letter to Theissen says the spores are not septate, but the oil drops are so close to each other that the appearance of a septum is given. In the specimens examined by the writer the spores have been clearly continuous.

Both Rehm (*l.c.*) and Theissen (17) have placed *Bolinia tubulina* as a synonym of *C. hypoxyloides*, but they are apparently in error in this assumption. According to Mr Mason the Fries specimen at Kew of *Sphaeria tubulina* has polystichous perithecia with elongate necks, and corresponds with the Fries (4) description of perithecia immersed and elongated into rounded necks. The name *Bolinia* was first created as a subgenus by Nitschke (11), and later given generic rank by Saccardo (14). Nitschke apparently did not have a Fries specimen before him when he described *B. tubulina*, but had some other Swedish

specimen. He(11) says the perithecia characterise the group, are deeply sunken in the stroma and are drawn out into unusually long necks. This description approached that of Fries, and is certainly not a description of the material described by Karsten.

Theissen(17) also places *Nummularia lutea* (Alb. & Schwein.) Nits. and *N. gigas* Plowr. as synonyms of *C. hypoxyloides*. He is also in error in this, because both of these forms have rounded or ovate perithecia drawn out into long necks instead of the tubuliform perithecia of *Camarops*.

The Montagne specimen of *H. polyspermum* at Kew is, according to Mason in a letter, the same as his English specimen of *Camarops* which is equal to Karsten's *C. hypoxyloides*. As Montagne's (1856) description was prior to that of Karsten (1873) the correct name for this fungus should be *C. polyspermum* (Mont.).

1. ***Camarops polyspermum*** (Mont.) comb. nov.

Hypoxylon polyspermum Mont. in Sagra, *Hist. Nat. Cuba. Bot.* (1842), p. 345.

Camarops hypoxyloides Karsten, *Myc. Fenn.* II (1873), p. 53.

Hypoxylon cylindrophorum Ell. & Everh. *Univ. Ia. Bull.* II (1893), pp. 394–415.

H. atroviride Ell. & Everh. in Herb. Morgan.

Solenoplea microspora Starb. *Ascom. d. I. Regn. Exp.* II; *Bihang t. K. Svenska Vet. Akad. Handlingar*, XXVII (1901), iii, n. 9, p. 13.

Type: *Hypoxylon polyspermum* Mont.

(Pl. VI, fig. 12.)

Stroma erumpent or superficial, applanate or rugose-undulate following the inequalities of the wood, solitary or coalescing, convex, indefinite in extent, 3–8 mm. thick; ectostroma thin, carbonaceous, ferruginous to almost black at maturity, penetrated by the umbilicate ostiolar necks; perithecia densely aggregated, filiform-cylindric or tubuliform, vertically oriented under the ectostroma, pallid-fuscous, 3–8 × 5–1 mm.; asci cylindric-tapering, copious, horizontally arranged in the perithecium, 30–50 μ long for the spore part and 20–30 μ for the stalk; ascospores uniseriate, elliptical with rounded ends, olivaceous to opaque, 5–6 × 2–3·5 μ.

The tubuliform perithecia with the very large umbilicate ostiola resemble the tubes of a polypore.

Apparently rare in Europe, but common in tropical America.

Solenoplea peltata Lloyd(8) from Porto Rico is closely related to this fungus, if not identical.

The specimens distributed by Ellis in Ell. & Everh. *N.A.F.* 2nd ed., no. 1788, and by Ravanel in *F. Amer.* nos. 346, 347, cited by Ellis under name of *H. polyspermum* Mont. are not that species, but are equal to *H. effusum* Nits.

Material examined.

Porto Rico Fungi no. 2726. (At Cornell.)
Morgan spec. (Under *H. atroviride*, at Univ. of Iowa.)
Ellis spec. (Under *H. cylindrophorum*, at N.Y. Bot. Garden.)
Miller no. 5941. (At Univ. of Georgia.)
Mason Herb. no. 105 England—no station on packet.

III. ***Daldinia*** Ces. & De Not. *Schema Sferiac. in Comm. Critt. Ital.* I (1863), p. 197.

Type species: *Sphaeria concentrica* Bolt.

Stroma erumpent, superficial, globose and plainly stipitate to hemispherical or effused and sessile; rubiginous, varying to shades of purple in age; context strikingly zonate, fibrous-woody, dark; perithecia borne in periphery of stroma, ovate to compressed, ostiola umbilicate; asci cylindrical, 8-spored, stalked; ascospores continuous, dark brown, inequilaterally elliptical; conidial layer borne on ectostroma, pulverulent, conidia hyaline to slightly coloured, continuous, minute.

This genus closely approaches the *Hypoxylon* concept and is separable only on the concentric zonation of the ectostroma, and that, as Theissen (17) suggests, is not absolute. Forms of *Daldinia placentiformis* (Berk. & Curt.) Theiss. are 1–2 cm. thick and plainly zoned, or a part of the same specimen may be very thin with no visible zones.

1. ***Daldinia concentrica*** (Bolt.) Ces. & De Not. *Comm. Critt. Ital.* I (1863), p. 198.

Sphaeria concentrica Bolt. *Fung. Halif.* append. (1791), p. 180, tab. 180.
Valsa tuberosa Scop. *Flor. Carniol.* 2nd ed. (1772), p. 399.
Sphaeria tunicata Tode, *Fung. Meckl. Sel.* II (1791), p. 59, tab. 17, f. 130.
S. fraxinea With. *Arrang. Brit. Pl.* 3rd ed. t. 4 (1796), p. 393.
S. concentrica Fr. *Syst. Myc.* II (1823), p. 331.
Hypoxylon concentricum Grev. *Scot. Crypt. Flora*, VI (1828), tab. 324.
H. concentricum Fr. *Summ. Veg. Scand.* (1849), p. 384

Type: Fries, Scler. Suec. no. 141.

(Pl. VI, fig. 2; Pl. VII, fig. 12.)

Stroma hemispherical to globose, sessile with wide base to contracted below and plainly stipitate, 2–4 cm. in diameter and 1–3 cm. thick, solitary or coalescing; young stroma rubiginous, erumpent from bark or superficial on decorticated wood, growing into one or more vertical stromata; entostroma conspicuously zonate, fibrous-woody, dark brown; ectostroma dark reddish purple, thin; perithecia monostichous, ostiola umbilicate; asci cylindric, 70–115 × 8–12 μ (p. sp.) with long stalk; ascospores uniseriate, elliptical to inequilateral, opaque at maturity, 12–17 × 6–9 μ; conidia ovate with greenish tint, continuous, 6–8 × 4–5 μ.

On *Fagus*, *Fraxinus* and *Betula* in Mason collection. Common throughout the world on many deciduous trees.

Nitschke (11) says the spores are 14–18 × 7–10 μ and Ellis (3) makes them 12–15 × 7–10 μ. The writer finds that most of the mature spores are about 15 × 8 μ. In a mount of this fungus there is extreme variation in spore ages, which accounts for the discrepancies in the spore dimensions given by different workers. Also the spores vary from very broadly elliptical to very narrow.

This species varies from *D. vernicosa* (Schwein.) Ces. & De Not. mainly in the structure of the entostroma. In the latter species this largely gelatinises at maturity, leaving white bands with hollow spaces between. Also *D. vernicosa* is shining black when mature. Theissen (17) makes *D. Eschscholzii* (Ehrh.) Rehm a synonym of *D. concentrica* var. *microspora* Starb., but the writer finds Rehm's type to have spores equal to typical *D. concentrica*, and so the former name should probably be listed as a synonym. Also *D. luzonensis* Rehm, according to part of the type in the writer's possession, has spores 12–15 × 5–7 μ, which would bring it within this species.

Material examined.

Fr. Scler. Suec. no. 141. (At Upsala. Compared by Nannfeldt.)

Fl. Lud. no. 2166. (At Cornell.)

Rav. F. Amer. no. 181. (At Cornell.)

Mason Herb. no. 13 Aviemore; no. 39 Norbury Park; no. 67 Rickmansworth; nos. 68, 69 Arundel.

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EXPLANATION OF PLATES.

PLATE VI.

Fig. 1. Ascus and spores of *Hypoxylon ustulatum*. Mason, no. 64.
Fig. 2. Ascus and spores of *Daldinia concentrica*. Mason, no. 68.
Fig. 3. Ascus and spores of *Hypoxylon serpens*. Mason, no. 31.
Fig. 4. Ascus and spores of *H. multiforme*. Mason, no. 5*b*.
Fig. 5. Ascus and spores of *H. cohaerens*. Mason, no. 62.
Fig. 6. Ascus and spores of *H. rutilum*. Mason, no. 54.
Fig. 7. Ascus and spores of *H. semi-immersum*. Mason, no. 95.
Fig. 8. Ascus and spores of *H. coccineum*. Mason, no. 46.
Fig. 9. Ascus and spores of *H. argillaceum*. Mason, no. 70.
Fig. 10. Ascus and spores of *H. fuscum*. Mason, no. 22.
Fig. 11. Ascus and spores of *H. rubiginosum*. Mason, no. 79.
Fig. 12. Ascus and spores of *Camarops polyspermum*. Mason, no. 105.
Fig. 13. Ascus and spores of *Hypoxylon luteum*. Mason, no. 14.

These drawings were made with the aid of a camera lucida. The magnification is 1000 diameters.

PLATE VII.

These photographs are all of natural size, showing macroscopic characters of stromata of the following:

Fig. 1. *Hypoxylon cohaerens*. The specimen to the right shows immature stromata and to the left mature.
Fig. 2. *Hypoxylon multiforme*. This shows the pulvinate form erumpent through the cracks of *Betula* bark.
Fig. 3. *Hypoxylon rutilum*. The pulvinate to semi-globose forms and the effused forms are shown.
Fig. 4. *Hypoxylon serpens*. Only the applanate form is shown.
Fig. 5. *Hypoxylon semi-immersum*. Mature stromata are to be seen on the right and immature ones on the left.
Fig. 6. *Hypoxylon ustulatum*. This is the common form which develops on uneven surfaces.
Fig. 7. *Hypoxylon coccineum*. Sometimes the stromata are much larger and connate.
Fig. 8. *Hypoxylon fuscum*. This is typical of the form seen on *Alnus* and *Corylus*.
Fig. 9. *Hypoxylon argillaceum*. The writer has seen no effused form of this species.
Fig. 10. *Hypoxylon rubiginosum*. This effused form is more common than the pulvinate form.
Fig. 11. *Hypoxylon luteum*. This shows several mature stromata.
Fig. 12. *Daldinia concentrica*. This form is found under good environment. A substipitate form is also common.

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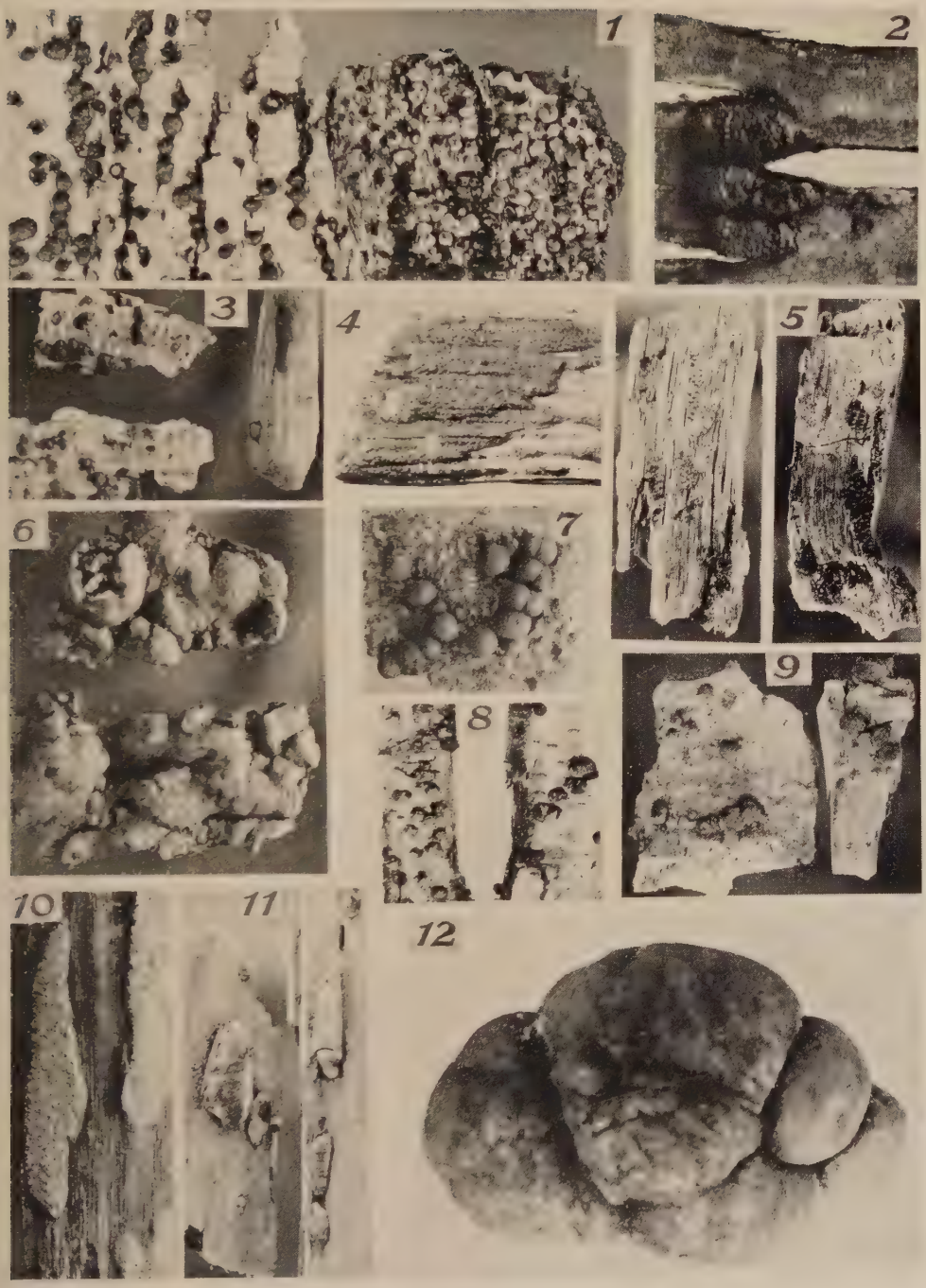
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A LIST OF FUNGI &c. MAINTAINED IN THE NATIONAL COLLECTION OF TYPE CULTURES, 1930.

By R. St John-Brooks and Mabel Rhodes.

In the 1923 *Transactions of the British Mycological Society* (1) appeared a list of the fungi and micro-organisms of economic importance maintained at that time in the National Collection of Type Cultures, comprising in all some three hundred and fifty species. These organisms represented fungi of importance in phytopathology, medical or veterinary science, technical and soil bacteriology and types useful for teaching purposes. Although this list was very incomplete and possessed many obvious lacunae it nevertheless appeared to be of assistance to mycologists and others at home and abroad.

A revised edition of the Catalogue of the National Collection (2) was published by the Medical Research Council in 1925 and was a complete reference to the bacteriological and mycological collections as then constituted, including, of course, those organisms of purely medical or veterinary interest. But owing to unavoidable causes the publication of an amended and contemporary list in these Transactions is considerably overdue. It is hoped that the following compilation, which comprises some seven hundred and seventy separate species out of the three thousand strains of bacteria and fungi of all kinds at present maintained at the Bureau, will stimulate enquiries for mycological and other cultures and at the same time induce colleagues at home and abroad to help in filling up such obvious gaps as still remain and to deposit important strains for maintenance and reference.

The staff of the Collection desire to take this opportunity of thanking mycologists and technical bacteriologists throughout the empire for many valuable additions to the collection since the last list was published and in this connection would wish to make special reference to the steady influx of important and interesting cultures during the past six years from the Director and Staff of the Imperial Bureau of Mycology.

The numbers given are the reference numbers of the cultures maintained in the collection and should be quoted in all applications for type cultures. The Curator and his staff will use their best endeavours to procure cultures of organisms which do not appear in the list, if they are required by correspondents. A small charge is made in most cases to cover cost of media, packing and postage.

All communications should be addressed to the Curator, National Collection of Type Cultures, Lister Institute, Chelsea Bridge Road, London, S.W. 3.

2791 Absidia capillata v. Tiegh.
1790 A. coerulea Bain.
1453 A. cylindrospora Hagem
3098 A. glauca (+) Hagem
3099 A. glauca (−) Hagem
2792 A. Regneri (Lucet & Cost.) Lendn.
1312 Acanthorynchus Vaccinii Shear
3015 Achorion Gallinae Sabrazés
3013 A. gypseum Bodin
3011 A. Quinckeanum Zopf
3012 A. violaceum Bloch.
706 Acladium Castellanii Pinoy
3145 Acremoniella olivaespora Ciferri & Ashf.
1491 Acrospeira mirabilis B. & Br.
1132 Acrostalagmus cinnabarinus Corda
3146 Acrotheca obovatum var. subcapitatulum Ciferri & Ashf.
2958 Acrothecium lunatum Wakker
1578 Actinomyces albosporeus Krainsky
1574 A. aureus Waks. & Curt.
2835 A. bovis Wolff & Isreal (anaerobic)
600 A. bovis Harz (aerobic)
1561 A californicus Waks. & Curt.
659 A. caprae Silb.
1569 A. chromogenus Gasp.
1564 A. Fradii Waks. & Curt.
1583 A. griseus Krainsky
1585 A. Lipmannii Waks. & Curt.
1566 A. pheochromogenus Conn
2744 A. praecox Millard & Burr
1565 A. reticuli Waks. & Curt.
1555 A. reticulus-ruber Waks.
1562 A. rutgersensis Waks. & Curt.
1356 A. scabies (Thaxter) Güssow
2745 A. Setonii Millard & Burr
2543 A. tumuli Millard & Beeley
1567 A. violaceus-ruber Waks. & Curt.
2746 A. viridis Millard & Burr
1580 A. virido-chromogenus Krainsky
1554 A. 96 Waks.
1582 A. 104 Waks.
1584 A. 128 Waks.
1586 A. 145 Waks.
1581 A. 168 Waks.
1560 A. 206 Waks.
1571 A. 218 Waks.
1313 Allescheria Boydii Shear (Human Pathogen.)
2863 Alternaria Citri Ellis & Pierce
2964 A. macrospora Zimm.
2925 A. Solani (Ell. & Mart.) Jones & Grout
605 Amylomyces Tapioca
1314 Anthostomella destruens Shear
1945 Aspergillus Amstelodami Mang.
595 A. candidus Link
1325 A. carbonarius (Bain.) Thom
978 A. clavatus Desm.
973 A. effusus Tiraboschi
596 A. flavus Link
1693 A. fumaricus Wehm.
982 A. fumigatus Fres.
2655 A. glaucus Link
1017 A. luchuensis Inui
795 A. nidulans (Eidam) Winter
594 A. niger v. Tiegh.
1692 A. niger-citricus Wehm.
979 A. ochraceus Wilh.
598 A. Oryzae (Ahlberg) Cohn
975 A. parasiticus Speare
1324 A. pulverulentus (McAlp.) Thom
794 A. repens de By.
2044 A. Schiemanni (Schiem.) Thom
980 A. Sydowi Bain. & Sart.
599 A. tamarii Kita
981 A. terreus Thom
974 A. terricola March. var. americana March.
1883 A. versicolor (Vuill.) Tiraboschi
597 A. Wentii Wehm.
2050 Atelosaccharomyces sp. Guilliermond
1855 Azotobacter chroococcum Beij.
612 Bacillus aceti Hansen
1068 B. acetoethylicum Northrop
2224 B. acetosum Henneberg
413 B. acidi-lactici Hueppe
1899 B. acidophilus Moro
2604 B. adhaerens Laubach
2598 B. agri Laubach & Rice
2601 B. albolactis Migula
2870 B. aminovorans den Dooren de Jong
1959 B. amylovorus (Burrill) Trevisan
1961 B. angulatum Fromme & Murray
1977 B. aptatum N. A. Br. & Jamieson
1987 B. aroideae Townsend
2590 B. aterrimus Lehm. & Neum.
1986 B. atrofaciens McCullough
1953 B. atrosepticus van Hall.
393 B. Barkeri (St. J.-B.) Berridge
1982 B. beticolum Smith, Brown & Townsend

2611 B. brevis Migula
76B. B. bulgaricus Grigoroff
619 B. butylicus Weizm.
1650 B. butyricus Hueppe
2314 Bacterium C. Chaston Chapman
2690 B. calidolactis Hammer
1958 B. campestre Pammel
1956 B. cannae Bryan
1975 B. caratovorus Jones
1381 B. caryocyaneus Beij.
2599 B. cereus Frankland
2600 B. cereus Frankland var. fluorescens Laubach
2610 B. circulans Jordan
408 B. cloacae Jordan
2584 B. closteroides Gray & Thorn.
2596 B. cohaerens Gottheil
86 B. coli-communis Esch.
419 B. communior Durham
1652 B. corallinus Heff.
1971 B. coronafaciens Elliott
2572 B. cycloclastes Gray & Thorn.
2375 B. Delbrückii (Leichm.) Henneberg
1955 B. Delphinii E. F. Smith
927 B. dendroides Holzmüller
1656 B. denitrificans Burri & Stutz
1385 B. denitrofluorescens liquefaciens Kluyver
964 B. fluorescens liquefaciens Flügge
912 B. fluorescens non-liquefaciens Lehm. & Neum.
1174 B. fulvum Zimm
2608 B. fusiformis Gottheil
2687 B. globiformis Conn
2593 B. Globigii Migula
1965 B. gummisudans L. McCullough
661 B. Güntheri Lehm. & Neum.
2880 B. herbicola Burri & Düggeli
387 B. Hyacinthi Wakker
2847 B. indicus-ruber Koch
2575 B. iopagum Gray & Thorn.
2832 B. Juglandis (Pierce) E. F. Smith
2689 B. kaustophilus Prickett
614 B. Kützingianum Hansen
1957 B. lachrymans E. F. Smith & Bryan
418 B. lactis aerogenes Escherisch
2613 B. laterosporus Laubach
389 B. Lathyri Manns & Tauberhaus
1960 B. malvacearum E. F. Smith
1981 B. marginale N. A. Brown
2605 B. megatherium de By.
2589 B. mesentericus (Flügge) Migula
2595 B. mesentericus (Flügge) Migula var. flavus Laubach
1360 B. methanicus Söhn.
1962 B. michiganense E. F. Smith
1966 B. Mori Boy. & Lam.
2794 B. mucosus capsulatus
2602 B. mycoides Flügge
2736 B. niger Migula
1970 B. panici Elliott
2594 B. panis Migula
2686 B. parvulum Conn
613 B. Pasteurianum Hansen
1978 B. Pelargoni N. A. Brown
2608 B. petasites Gottheil
1968 B. Phaseoli E. F. Smith
1972 B. Phaseoli E. F. Smith var. sojense E. F. Smith
2653 B. phosphorescens Fischer
1985 B. phytophthorus Appel
2603 B. Prausnitzii Trevisan
1404 B. prodigiosus Cohn
394 B. proteamaculans Paine
401 B. proteus-vulgaris Hauser
405 B. proteus-zenkeri Hauser
1963 B. Pruni E. F. Smith
2609 B. pseudotetanicus (Krause) Migula
1999 B. pyocyaneus Flügge
1376 B. radiobacter (Beij.) Lohnis
1655 B. rossicum Kell.
2796 B. rubefaciens Burr
2597 B. simplex Gottheil
385 B. solanisaprus Harrison
1969 B. Stewarti E. F. Smith
2795 B. suberfaciens Burr
2586 B. subtilis (Ehrenb.) Cohn
2587 B. subtilis-viscosus Chester
2813 B. synxanthus (Ehrenberg) Lehm. & Neum.
1974 B. Syringae (Van Hall) E. F. Smith
1964 B. tabacum Wolf & Foster
2881 B. tenue Ehrenberg
2612 B. terminalis Migula
2688 B. terminalis Migula var. thermophilus Prickett
2812 B. thermophilus Nègre
392 B. Tolaasi Paine
1983 B. tracheiphilus E. F. Smith
1967 B. trifoliorum E. F. Smith
1490 B. Truffautii Truffaut & Bezssonoff
1976 B. tumefaciens Smith & Townsend
2607 B. tumescens Zopf
1654 B. ureae Leube
2213 B. vascularum (Cobb) R. G. Sm.
1980 B. viridilividum N. A. Brown
1979 B. vitians N. A. Brown
620 B. volutans Thaysen
2588 B. vulgatus (Flügge) Trevisan
972 Bacterium "X" A. Br.
1648 B. xylinum A. Br.
3100 Basidiobolus ranarum Eidam
1801 Beauveria Bassiana (Bals.) Vuill.
1659A. B. densa (Link) Picard
2227 B. sp. aff. densa. Fly, Ceylon
1142 B. globulifera (Speg.) Picard
2226 B. stephanoderis (Bally) Petch

2706 Betacoccus arabinosaceus Orla-Jensen
3128 Blakeslea trispora (+) Thaxt.
3129 B. trispora (–) Thaxt.
3147 Blastodendrion intermedium Ciferri & Ashf.
1642 Blastomyces "Sydney." (Human pathogen.)
1641 B. "M.H." (Human pathogen.)
2787 Blastomycoides dermatitidis (Gilch. & Stokes) Cast. (Human pathogen.)
2788A. B. tulanensis Castell. (Human pathogen.)
2805 Blepharospora cambivora Petri
2523 Bodinea violacea (Bodin) Ota & Langer.
1261 Botryosporium longibrachiatum (Oud.) Maire
1494 Botrytis Allii Munn
852 B. cinerea Pers.
1189 B. cinerea Pers. Biological strain (fig)
1075 B. cinerea Pers. Biological strain (quince)
2712 B. narcissicola Klebh.
1138 B. Paeoniae Oud.
2713 B. polyblastis Dowson
1448 B. pyramidalis (Sacc.) Johnson
1496 B. Tulipae (Lib.) Hopk.
1832 Boudiera Claussenii Henn.
2811 Brettanomyces Claussen sp.
2201 Calonectria graminicola B. & Br.
1740 Candida breve Berkh.
1739 C. Chodati Berkh.
2135 Caseococcus Gorini
1222 Catenularia fuliginea Saïto
1603 Cephalosporium Asteris Dowson
1859 C. longisporum Petch
1145 C. Sacchari Butl.
1131 Cephalothecium roseum Corda
1364 Cercosporella Antirrhini Wakef.
2517 Cercosporina Kikuchii Matsumoto
1315 Ceuthospora lunata Shear
3184 Chalara mycoderma Bonord.
3109 Chlamydomyces palmarum (Cooke) Mason
2801 Choanephora cucurbitarum (+) (B. & Rav.) Thaxt.
2802 C. cucurbitarum (–) (B. & Rav.) Thaxt.
3074 Chromobacterium cohaerens Grimes
3073 C. hibernicum Grimes
2537 C. violaceum Bergonzoni
2416 C. viscosum Grimes
2968 Ciliospora gelatinosa Zimm.
1791 Circinella minor Lendn.
2793 C. spinosa v. Tiegh. & Le Monn.
606 Citromyces B. Wehm.
1182 Cladosporium fulvum Cooke
2278 C. herbarum Link
2783 C. Mansoni Castell.
3043 Clasterosporium maydicum Sacc.
2264 Clostridium Beijerincki Donker
1649 C. Pasteurianum Winogr.
2263 C. pectinovorum Beij. & van Delden
1380 C. polymyxa Prazm.
883 Coccidioides immitis Rixf. & Gilchr. (Human pathogen.)
1947 Colletotrichum Camelliae Mass.
1006 C. Lindemuthianum (Sacc.) Bres.
1194 C. linicolum Pethyb. & Laff.
1130 C. phomoides (Sacc.) Chester
2312 Coniophora cerebella Alb. & Schwein.
1948 Coniothecium chromatosporum Corda
1768 Coniothyrium convolutum Horne & Horne
3096 Corticium Solani Prill. & Delacr.
2075 Cryptococcus Castellanii Re.
767 C. farciminosus Rivolta & Micellone
2077 C. graciloides Castell.
1869 C. macroglossiae Castell.
2772 C. metaniger Castell.
2774 C. pararoseus Castell.
2773 C. rubrorugosus Castell.
1792 Cunninghamella echinulata Thaxt.
3101 C. elegans (+) Lendn.
3102 C. elegans (–) Lendn.
2511 Cylindrocarpon Mali (All.) Wr.
1294 Cytosporina ludibunda Sacc.
1184 C. Ribis P. Magn.
477 Debaryomyces globosus Klöck.
2059 D. Klöckeri Guill. & Péju.
2048 D. tyrocola Konokotin
1547 Dematium pullulans de By.
1682 Diaporthe perniciosa March. Forma Pruni Cayley
1358 Diplodia Corchori Syd.
1474 D. natalensis Evans
1133 Diplodina Lycopersici (Cooke) Hollós
1766 Eidamia catenulata Horne & Williamson
1765 E. tuberculata Horne & Jones
1764 E. viridescens Horne & Williamson
555 Emmentald coccus (cheese)
703 Endodermophyton indicum Castell.
1758 E. tropicale Castell.
1871 Endomyces fibuliger Lindn.
1908 E. Hordei Saito
2045 E. Lindneri Saito
2241 E. vernalis Ludwig
2700 Epidermophyton cruris Castell.
3016 E. Perneti Castell.

702 E. rubrum Castell.
1824 Eurotiopsis Gayonii Cost.
2311 Fomes annosus Fr.
2169 F. pinicola (Fr.) Cooke var. marginalis
986 Fumago vagans Pers.
1770 Fusarium acuminatum (Ell. & Everh.) Wollenw.
2710 F. avenaceum (Fr.) Sacc.
1141 F. coeruleum (Lib.) Sacc.
2709 F. culmorum (W. G. Sm.) Sacc.
2735 F. culmorum (W. G. Sm.) Sacc. var. leteius Sherbak.
1136 F. Dianthi Prill. & Delacr.
3097 F. fructigenum Fr.
2711 F. herbarum (Corda) Fr.
2862 F. javanicum Koorders
2509 F. juruanum P. Henn
1081 F. Lini Bolley
1887 F. Malli Taub.
1886 F. Solani Mart.
1296 F. sporotrichoides Sherbak.
1696 F. vasinfectum Atk.
1890 Gibberella Saubinetii (Mont.) Sacc.
1454 Glíocladium penicillioides Corda
2513 Gloeosporium fructigenum Berk.
1839 G. nervisequum (Fuck.) Sacc.
1800 Glomerella cingulata (Lath.) Spauld. & von Schenk
1317 G. rufomaculans Vaccinii Shear
1861 Gonatorrhodiella coccorum Petch
2951 Granulobacter pectinovorum Beij. & van Delden
2527 Grubyella (Achorion) Schönleinii (Lebert) Ota & Langer.
1318 Guignardia Vaccinii Shear
817 Hansenia apiculata (Reess) Lindn.
816 H. apiculata Schmitz
478 Hanseniaspora valbyensis Klöck.
1793 Helicostylum pyriforme Bain.
1319 Helminthosporium inaequale Shear
1357 H. Sacchari Butl.
1888 H. sativum Pam., King & Bakke
2778 Hemispora pararugosa Castell., Douglas & Thomp.
705 H. rugosa Castell.
2769 H. stellata Vuill.
2186 Hendersonia Sacchari Butl.
1137 Heterosporium echinulatum (Berk.) Cooke
2893 Hormodendrum Langeroni da Fonseca, Leão & Penido
2957 Isaria farinosa (Dicks) Fr.
947 Lactobacillus pentoaceticus Fred, Peterson & Davenport
2170 Leptothrix. (Human pathogen.)
3027 Malassezia Baillon sp. from Tinea flava
2185 Melanospora pampeana Speg.
1862 M. parasitica Tul.
2309 Merulius lacrymans Fr.
1660 Metarrhizium anisopliae (Metsch.) Sor.
2678 Micrococcus agilis Ali-Cohen
1630 M. aurantiacus Cohn
1627 M. badius Lehm. & Neum.
1657 M. candicans Flügge
1628 M. concentricus Zimm.
2677 M. conglomeratus Migula
1629 M. flavus (Flügge) Lehm. & Neum.
2679 M. Freudenreichii Guillebeau
2680 M. luteus (Schröt.) Cohn
2558 M. piltonensis Gray & Thorn.
2682 M. rhodochrous Zopf
1114 M. roseus (Bumm.) Lehm. & Neum.
2559 M. sphaeroides Gray & Thorn.
1631 M. sulphureus Zimm.
2684 M. ureae Cohn
2685 M. varians Migula
3090 Microcyclus aquaticus Ørskov
1749 Microspira agarliquefaciens Gray & Chalmers
3008 Microsporum equinum Bodin
3009 M. ferrugineum Ota
3007 M. fulvum Uriburu
2106 M. Japon Kambayashi
2279 M. parasiticum
2280 M. sarcinula
714 Monilia albicans (Robin) Zopf
2855 M. Ashfordii Castell.
2856 M. butantanensis Castell.
922 M. candida Bon.
2146 M. from "cutworm." Pospolov
2858 M. fusca Browne
2850 M. javanica Went & Geerligs
698 M. kruzei Castell.
697 M. macedoniensis Castell.
2776 M. metalondinensis Castell.
2851 M. nigra Burri & Staub
2853 M. parapsilosis Ashford
707 M. Pinoyi Castell.
2775 M. pseudotropicalis Castell.
1065 M. psilosis Ashford
2505 M. from tongue. (Human pathogen.)
696 M. tropicalis Castell.
2755 M. variabilis Lindn.
1446 Monosporium acuminatum Bon. v. terrestre Sacc.
3105 Mortierella Candelabrum van T. & Le Monn.
3150 M. niveovelutria Ciferri & Ashf.
3106 M. reticulata van T. & Le Monn.
1903 Mucor alternans v. Tiegh.
1904 M. erectus Bain.
2010 M. hiemalis (+) Wehm.

2011 M. hiemalis (—) Wehm.
1901 M. javanicus Wehm.
1121 M. lusitanicus Brüderlein
3103 M. Mucedo (+) Linn.
3104 M. Mucedo (—) Linn.
2173 M. piriformis Fischer
1123 M. plumbeus Bon.
1902 M. pusillus Lindt
1122 M. racemosus Fres.
921 M. Rouxii Wehm.
1126 M. sphaerosporus Hagem
1821 M. spinosus v. Tiegh.
2571 Mycobacterium actinomorphum Gray & Thorn.
2562 M. agreste Gray & Thorn.
1470 M. album Söhn.
2570 M. coeliacum Gray & Thorn.
2568 M. convolutum Gray & Thorn.
2566 M. crystallophagum Gray & Thorn.
2569 M. erythropolis Gray & Thorn.
2761 M. globerulum Gray
1472 M. lacticola Söhn.
1469 M. luteum Söhn.
2874 M. opacum den Dooren de Jong
525 M. phlei (Möller) Lehm. & Neum.
1471 M. phlei Söhn.
1468 M. rubrum Söhn.
2873 M. salmonicolor den Dooren de Jong
526 M. Stercusis (Möller's "Mist" Bacillus)
1849 Mycoderma arborescens Kufferath
1848 M. Bordetii Kufferath
819 M. cerevisiae Desm., Hansen
2055 M. Chevalieri Guill.
3021 M. cutaneum Ota (Human pathogen.)
2561 Mycoplana bullata Gray & Thorn.
2560 M. dimorpha Gray & Thorn.
1842 Mycotorula famata Harrison
1843 M. vesica Harrison
1846 Nadsonia fulvescens Syd.
1143 Nectria diversispora Petch
1795 N. Ipomoeae Hals.
2209 Nematospora Coryli Pegl.
2208 N. Gossypii Ashby & Nowell
2500 Nigrospora Oryzae (B. & Br.) Petch
2393 Nocardia africana Pijper & Pullinger
1934 N. caviae Snijders
1935 N. Cuniculi Snijders
800 N. Dassonvillei Broque-Rousseau
1070 N. indica Kanth.
576 N. lutea Christoph. & Arch.
3042 N. macropodidarum
3026 N. Pelletieri (Laveran) Pinoy
2391 N. pretoriana Pijper & Pullinger
2781 N. rubra Carabo
2392 N. transvalensis Pijper & Pullinger
700 Oidium asteroides Castell.
3087 O. sp. Chaston Chapman (from factory effluent)
1886 O. lactis Fres.
1825 O. Lupuli Matthews & Lott
2777 O. matalense Castell.
701 O. rotundatum Castell.
2103 Omphalia flavida (Cke.) Maubl. & Rangel
1742 Oospora fragrans (Krz.) Berkh. var. minuta Berkh.
1743 O. humi (Mazé) Berkh.
1241 Paecilomyces Bain. sp.
1062 Parasaccharomyces Ashfordi Anderson
984 Penicillium avellaneum Thom & Turesson
580 P. brevicaule Sacc.
581 P. brevicaule Sacc. var. album Thom
582 P. camemberti Thom
583 P. camemberti Thom var. Rogeri Thom
602 P. candidum Link
589 P. chrysogenum Thom
1718 P. claviforme Bain.
3089 P. divaricatum Thom
587 P. Duclauxi Delacr.
1719 P. elongatum Link
593 P. expansum Link
763 P. glaucum Link
1720 P. granulatum Bain.
1721 P. herquei Bain.
584 P. lilacinum Thom
585 P. luteum Zukal
3127 P. notatum Westl.
983 P. oxalicum Currie & Thom
1722 P. patulum Bain.
1151 P. pinophilum Hedgcock
586 P. purpurogenum Fleroff
588 P. roqueforti Thom
1730 P. roseum Link
592 P. rugulosum Thom
3029 P. solitum Westl.
591 P. spinulosum Thom
1299 Pestalozzia palmarum Cooke
1259 P. Theae Sawada
1776 Phialophora verrucosa Medler (Human pathogen.)
1135 Phoma alternariaceum Brooks & Searle
1950 P. Betae Frank
2656 P. Lingam (Tode) Desm.
1798 P. Pomi Pass.
1383 Photobacterium phosphorium Beij.
2894 Phycomyces nitens (+) Kunze
2895 P. nitens (—) Kunze
1444 Phyllostica prunicola Sacc.

1799 Physalospora Cydoniae Arnaud
2807 Phytophthora Arecae (Colem.) Pethyb.
3062 P. Boehmeriae Sawada
2082 P. Cactorum (Lib. & Cohn) Schröt.
3061 P. Capsici Leon.
2802 P. Cinnamomi Rands
3057 P. citricola Saw.
3134 P. Colocasiae Rac.
2803 P. cryptogoea Pethyb. & Laff.
2069 P. erythroseptica Pethyb.
1193 P. Fagi Hart.
3058 P. hydrophila Curzi
3088 P. infestans de By.
2808 P. Meadii McRae
3063 P. melongenae Saw.
3059 P. mexacana Hotson & Hartge
1751 P. palmivora Butl.
3132 P. palmivora Butl. Rubber group
3133 P. palmivora Butl. Cacao group
2080 P. parasitica Dastur
2809 P. Pini Leon.
2806 P. Richardiae Buis.
3055 P. Syringae Klebahn
3060 P. Tabaci Saw.
481 Pichia alcoholophilia Klöck.
483 P. calliphorae Klöck.
901 P. farinosa Lindner-Hansen
479 P. membranaefaciens Hansen
480 P. polymorpha Klöck.
482 P. suaveolens Klöck.
3107 Piptocephalis sp.
3025 Pityrosporum rhinoseroso
1761 Polyopeus aureus Horne
2310 Polyporus sulphureus (Bull.) Fr.
1004 Polyspora Lini Laff.
2875 Protominobacter albo-flavum α den Dooren de Jong
2876 P. albo-flavum β den Dooren de Jong
2877 P. albo-flavum γ den Dooren de Jong
2878 P. albo-flavum δ den Dooren de Jong
2879 P. rubrum den Dooren de Jong
3151 Prototheca portoricensis Ciferri & Ashf.
1352 P. portoricensis var. trispora Ciferri & Ashf.
2872 Pseudomonas aminovorans den Dooren de Jong
2870A. P. aminovorans α den Dooren de Jong
2870B. P. aminovorans β den Dooren de Jong
2871 P. aminovorans γ den Dooren de Jong
2580 P. cruciviae Gray & Thorn.
933 P. (denitrifying)
2578 P. desmolyticum Gray & Thorn.
2760 P. indoloxidans Gray
2576 P. pictorum Gray & Thorn.
2196 P. radicicola Beij.
2577 P. rathonis Gray & Thorn.
499 Pseudosaccharomyces africanus Klöck.
490 P. antillarum Klöck.
497 P. apiculatus Reess
492 P. austriacus Klöck.
485 P. coricis Klöck.
491 P. germanicus Klöck.
487 P. indicus Klöck.
498 P. javanicus Klöck.
494 P. Jensenii Klöck.
489 P. Lafari Klöck.
1816 P. Lindneri Klöck.
484 P. malaianus Klöck.
496 P. Mülleri Klöck.
486 P. occidentalis Klöck.
493 P. santacruzensis Klöck.
488 P. Willii Klöck.
1745 Pullularia nigrans Berkh.
3053 Pyronema domestica (Sow.) Sacc.
2810 Pythium complectens Braun
3067 P. papillatum Matthews
2652 P. splendens Braun
1175 Rhizoctonia destruens Tassi
1949 R. lamellifera Small
1464 R. Solani Kühn
1905 Rhizopus japonicus Vuill.
3108 R. nigricans (+) Ehrenb.
2419 R. nigricans (−) Ehrenb.
1907 R. Oryzae Went & Geer.
1906 R. tonkinensis Vuill.
2466 R. Tritici Saito
907 Rhodotorula plicata Harrison
241A. R. rutila Harrison
2526 Sabouraudites Audouini (Gruby) Ota & Langer.
2524 S. felineus (Fox & Blaxall) Ota & Langer.
2525 S. lanosus (Sab.) Ota & Langer.
1808 Saccharomyces brasiliensis Lindn.
742 S. carlsbergensis Hansen
815 S. cerevisiae Hansen (Baking Yeast)
2160 S. cerevisiae Hansen (Brewing Yeast)
2779 S. cerevisiae Hansen (Distilling Yeast)
2054 S. Chevalieri Guill.
467 S. ellipsoideus Hansen
812 S. exiguus (Reess) Hansen
3139 S. festinans Ward & Baker
905 S. fragilis Jörgensen
1681 S. Hansenii Zopf
1809 S. Ilicis Grönland
469 S. intermedius Hansen
2053 S. Lindneri Guill.
472 S. Marxianus Hansen
743 S. monacensis Hansen
2049 S. muntzii

468 S. Pastorianus Hansen
1071 S. pyriformis Marshall Ward
1015 S. saké Yabe
790 S. thermantitonum Johnson
471 S. turbidans Hansen
470 S. validus Hansen
473 Saccharomycodes Ludwigii Hansen
814 Saccharomycopsis capsularis Schiönn.
952 Sarcina aurantiaca Flügge
611 S. lutea Flügge
2768 Scedosporium apiospermum Sacc. (Human pathogen.)
1014 Schizosaccharomyces mellacei Jörgensen
382 S. octosporus Beij.
902 S. Pombé Lindn.
476 Schwanniomyces occidentalis Klöck.
1238 Sclerotinia cinerea Schröt. forma Mali
1239 S. cinerea Schröt. forma Pruni
2198 S. erythroniae Whetzel
1072 S. fructigena (Pers.) Schröt.
1074 S. sclerotiorum (Lib.) Bref.
1593 S. trifoliorum Erikss.
1076 Sclerotium cepivorum Berkh.
2516 S. fulvum Fr.
2714 S. Gladioli Massey
1262 S. Rolfsii Sacc.
1497 S. Tuliparum Kleb.
2965 Scolecobasidium constrictum Abbott
3171 Scopulariopsis sp. From Bullfrog
1891 Septoria Lycopersica Speg.
2210 Spermophthora Gossypii Ashby & Nowell
2864 Sphaeropsis malorum Peck
3068 Sphaerostilbe aurantiaca Tub.
1860 Spicaria javanica Bally
1750 Spirochaeta cytophaga Hutch.
2959 Spondyocladium xylogenum A. L. Smith
3017 Sporotrichum Beurmanni Matr. & Ram.
1672 S. carnis Brooks & Hansford
3020 S. equinum
3019 S. Gougeroti Matr.
406 S. Schenckii Perkins
963 Staphylococcus cremoris-viscosi Hammer & Cordes
1183 Stereum purpureum Fr.
1716 Sterigmatocystis flavipes Bain.
662 Streptococcus acidi-lactici Grot.
2701 S. bovis Orla-Jensen
2702 S. glycerinaceus Orla-Jensen
2705 S. liquefaciens Orla-Jensen
658 Streptothrix Bert-Leishman
2300 S. coelicolor Reiner Müller
630 S. from foal
1129 Stysanus stemonites (Pers.) Corda
3155 Syncephalastrum cinereum Bain.
1794 S. racemosum Cohn
2699 Tetracoccus casei Orla-Jensen
2672 Thamnidium chaetocladioides Bref.
1127 T. elegans Link
1889 Thielavia basicola (B. & Br.) Zopf
1223 Thielaviopsis ethaceticus Went
1260 T. paradoxa (de Seynes) von Höhn.
3136 Thiobacillus thioxidans Waks. & Joffe
2630 Torula acclotiana Kufferath
2635 T. aerius Saito
2639 T. alactosa Kluyver
2638A. T. aurantiaca Saito
2647 T. aurea Saito
1671 T. botryoides Brooks & Hansford
2052 T. colliculosa Hartmann
1134 T. convoluta Harz
2625 T. corallina Saito
1302 T. cremoris Hammer & Cordes
2641 T. dattila Kluyver
2626 T. fermentati Saito
2643 T. flava Saito
1746 T. fuliginea Berkh.
2640 T. galactosa Kluyver
2648 T. glutinis (Cohn) Pringsheim & Bilewsky
2634 T. gropengiesserii Harrison
2636 T. heveanensis Groenwege
1492 T. histolytica Freeman & Weidman
2645 T. holmii Jörgensen
2637 T. lactosa Kluyver
1847 T. laurentii Kufferath
2646 T. lipofera den Dooren de Jong
2624 T. lipolytica Jacobsen
2623 T. mineralis Haydruck & Haehn
2644 T. minuta Saito
2622 T. mucilaginosa Jörgensen
3024 T. mycetoma
885 T. nasalis Harrison
2632 T. pulcherrima Lindn.
2628 T. rubescens Saito
2627 T. rubra Saito
2649 T. rubra Schimon.
2631 T. rufula Saito
2642A. T. rugosa Saito
2629 T. sanguinea Schimon
1303 T. spherica Hammer & Cordes
2046 Torulaspora fermentati Saito
2051 T. Rosei Guill.
3153 Torulopsis minuta (Saito) Ciferri var. parvissima Ciferri & Ashf.
3154 T. nitritophila Ciferri & Ashf.
704 Trichophyton balcaneum Castell.

3000 T. cerebriforme Sabour.
2784 T. decalvans Castell.
3004 T. depressum MacCarthy
2992 T. effractum Sabour.
2996 T. equinum Matr. & Dassonv.
2993 T. faviforme-album Sabour.
2995 T. faviforme-discoides Sabour.
2994 T. faviforme-ochraceus Sabour.
2997 T. fumatum Sabour.
2991 T. glabrum Sabour.
3002 T. gypseum-asteroides Sabour.
3003 T. gypseum-granulosum Sabour.
3001 T. gypseum-lacticolor Sabour.
2786 T. Louisianicum Castell.
2785 T. nodoformans Castell.
2998 T. persicolor Sabour.
2999 T. plicatile Sabour.
2521 T. Sabouraudii R. Blanchard
2522 T. sulphureum Fox
2520 T. tonsurans Malmsten
2121 Tyrothrix distortus Duclaux
2120 T. filiformis Duclaux
2123 T. geniculatus Duclaux
2122 T. minimus Duclaux
2116 T. scaber Duclaux
1116 T. tenuis Duclaux
2211 Ustilago Zeae Beck
2363 Venturia inaequalis Aderh.
1180 V. pirina Aderh.
2508 Vermicularia Dematium (Pers.) Fr.
2506 V. Eryngii Corda
2507 V. trichella Fr.
2512 Verticillium alboatrum Reinke & Berth.
2583 Vibrio cuneata Gray & Thorn.
2581 V. cyclosites Gray & Thorn.
2582 V. neocistes Gray & Thorn.
1937 V. percolans Mudd & Warren.
1070 Wardomyces anomala Brooks & Hansford
474 Willia anomala Hansen
1546 W. belgica Lindn.
475 W. Saturnus Klöck.
2404 Yeast (Californian Wine)
1879 Y. (Cider)
903 Y. (Frohberg)
1806 Y. (Johannisberg II) Wortmann
904 Y. (Kefir) Hansen
607 Y. (Lactose-fermenting)
909 Y. (Logos)
1639 Y. (Mahua)
1467 Y. (Mineral "Futterhefe")
1346 Y. (Pink)
2031 Y. (Rasse XII)
906 Y. (Saaz)
608 Y. (Sternberg "675")
2403 Y. (Tokayer)
813 Zygosaccharomyces Barkeri Sacc. & Syd.
2047 Z. bisporus Naganishi
2057 Z. Nadsonii Guill.
2058 Z. Pastorianus Guill.
2405 Z. priorianus Klöck.

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OBSERVATIONS ON THE REPRODUCTION AND FUNGAL ENDOPHYTISM OF LUNULARIA CRUCIATA (L.) DUMORTIER.

By Theodora B. Auret, B.Sc.

(With eight Text-figures.)

Material of the liverwort *Lunularia cruciata* (L.) Dumortier* was collected from a spruit which runs through the University grounds at Milner Park, Johannesburg. An examination of

* *Marchantia cruciata* L. Sp. Pl. 1137 (1753) = *Lunularia cruciata* Dumortier. Identification made by Dr T. R. Sim of Maritzburg, Natal.

material collected in August, 1925, showed that archegonia but no antheridia were present.

It is worthy of note that only the archegonial plants of *Lunularia* are found in South Africa. Archegonia were present in clusters on a short projection from the dorsal surface of the thallus near the growing-point. The outgrowth varied from conical to reniform and archegonia were often mature with the egg showing clearly. Subsequent examination showed that no further development took place, and that the entire group of female organs dries up. The plants in the spruit were closely and carefully observed for nearly two years and observations in the second year, 1927, confirmed those of 1926.

Dr Sim suggested that this *Lunularia* may have more than one form, but that such was, as yet, unknown. Goebel (1905) mentions that when male plants are absent from dioecious forms of Hepaticae, it is a matter of course that these plants are not fertile, but he mentions that *Lunularia vulgaris* represents this in a very striking manner. For a long time this liverwort has been known in northern Europe as the female plant only, which is thought to have been introduced in orange casks from southern Europe. It has increased by gemmae and, although groups of archegonia are produced, no sporogonia have been found. He states that the male plant is not rare in the south of Europe, and suggests that the scarcity of the fruiting stage in Italy is due to there being usually insufficient water for fertilisation, as when cultivated at Munich the plants were found to fruit abundantly.

The male plant is unknown in South Africa and Dr Sim (1926) states that the female inflorescence had not been seen till 1924 in material from Orangezicht, Cape Town. The plants are propagated by gemmae only which are luxuriantly produced.

Microscopic examination showed that the thallus contained fungal hyphae. The physical nature of the soil on which this liverwort was found differed markedly in different areas, and the amount of fungus in the tissues of the gametophyte seemed to be correlated with these differences in habitat.

Historical notes.

The study of "*mycorrhiza*" has received much attention and very clear historical surveys are given by Rayner (1915) and Ramsbottom (1921). The term has been extended to include liverworts where fungal hyphae are found in association with thalli, although this use is not strictly accurate.

In view of a paper by Cavers (1903) and one by Ridler (1922) it seems unnecessary to repeat the accounts of previous workers

concerning the occurrence of fungal mycelium in the Hepaticae. That a fungus was present in liverworts was noted by Leitgeb as early as 1874. Cavers carried out investigations with a great number of Hepaticae and suggested that where sporogonia of Bryophytes are invaded the relation between fungus and host plant is one of parasitism, but where the gametophyte, in both thalloid and foliose liverworts, contains fungal hyphae the association is sometimes symbiotic.

Ridler (1922–3) described a fungus in *Pellia epiphylla* (L.) Corda, where infection was recorded in both the gametophyte and the sporophyte. In the latter it caused a disease, often killing the host tissues. The endophyte produced vesicles, arbuscules and sporangioles in the tissues of the gametophyte.

Ridler (1923) also described a fungus present in *Lunularia*.

Nicolas (1924) found male plants of *Lunularia* which were infected, and no mycelium in neighbouring sterile plants. The possibility of establishing a causal connection between these two phenomena proved to be invalid, as subsequent examination showed some male plants which were free from mycelial invasion.

Locality and nature of the soil where *Lunularia cruciata* was found.

The spruit at Johannesburg where the material occurs is in the nature of a storm-water stream with a certain amount of sewage. The liverwort is more abundant on certain parts of the bank than on others, growing quite low down near the water. Material examined was collected from these different parts and samples of soil from the particular areas were carefully analysed. The soil was found to be a clay loam, there being considerably more clay than sand. Some samples were found to contain pebbles and fair-sized fragments of rock. Although the external appearance of the liverwort was always similar, microscopic examination of the thallus indicated a marked difference in the amount of fungal hyphae present. When growing on pebbly soil the liverwort contained fewer hyphae. Although the physical nature of these soils differed, observations on the hydrogen-ion concentrations, which were measured colorimetrically with phenol red, showed that the *p*H value was the same—8·0–8·1. The quantity of fungal hyphae in the thallus, therefore, appears to be determined by the physical nature of the substratum. Moreover, infected liverworts, *e.g.* *Pellia* examined by Ridler, have been found on soils where the *p*H value was slightly acid.

Occurrence and distribution of the endophyte in the liverwort.

Material was collected at frequent intervals, and after immediate examination some plants were grown in the greenhouse on soil from the spruit. They thrived very well under these conditions.

Plants were examined when the thalli produced archegonia, gemmae cups, and when no archegonia were present. With only

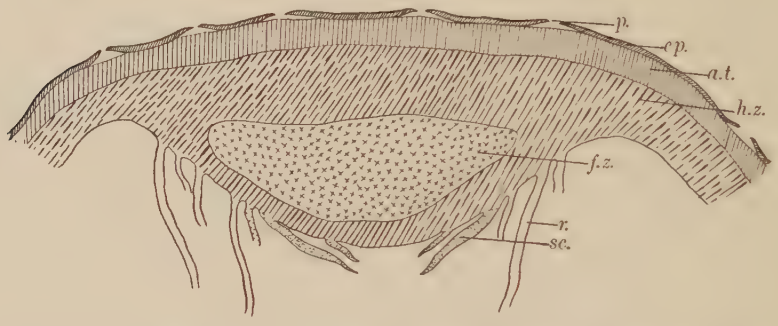

Fig. 1. Diagrammatic T.S. of thallus, showing moderate infection by the fungus. *p.* air pore; *ep.* epidermis; *a.t.* assimilating tissue; *h.z.* hyaline zone; *f.z.* fungal zone; *r.* rhizoid; *sc.* scale.

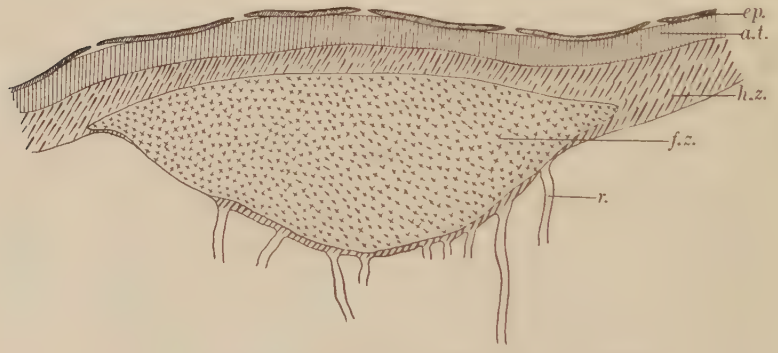

Fig. 2. Diagrammatic T.S. of thallus, heavily infected.

a few exceptions, the fungus was always present, some plants being more heavily invaded than others, the degree of infection varying with the nature of the soil. Series of sections through the thallus showed that the hyphae extended to within a few millimetres of the growing-point. The growth of the liverwort was luxuriant, plants were always green and apparently quite healthy. It was quite impossible to detect the presence of the

fungus without microscopic examination. This is a point of difference from *Fegatella conica* examined by Cavers (p. 33), where fungus-bearing plants were found to be larger and thicker than those free from hyphae. *Lunularia* was examined in longitudinal and transverse section, usually stained either with cotton blue and mounted in lacto-phenol or congo red and mounted in dilute glycerine. In all transverse sections, the hyphae were seen to be more densely packed along the midrib of the thallus. The fungus occupied a definite zone, being confined to the hyaline portion of the thallus. Not including the assimilating tissue or the upper epidermis, the thalli averaged from fifteen to thirty-five cells in thickness. In heavily infected plants, the fungus occupied almost the entire zone below the assimilating tissue, with the exception of the first two or three rows of cells immediately below; moreover the hyphae extended well to the sides of the thallus (Fig. 2). Plants not quite so heavily infected showed about eight rows of cells below the assimilating tissue and three or four rows below the fungal zone where no hyphae were present; here the extensions of the hyphae to the sides of the thallus were not so well defined (Fig. 1).

The hyphae apparently enter the liverwort through the rhizoids, as has often been suggested. Their occurrence in smooth rhizoids is common but rare in trabecular rhizoids. It was thought at first that only smooth rhizoids contained hyphae, but, though it is probable that the fungus gains entry into the tissues of the thallus through these only, trabecular rhizoids have been shown to be infected. It can readily be seen why these were thought to be free from infection when sections of the thallus, which very rarely have whole rhizoids attached to the ventral surface, were examined. Goebel (1905) states that plants arising from gemmae at first possess only smooth rhizoids which enter the soil directly and anchor the thallus. Trabecular rhizoids arise subsequently, retain a course along the ventral surface of the thallus and enter the soil only at some distance from their actual origin. Therefore, it might be expected that when hyphae occur in trabecular rhizoids they would be found in the portions furthest away from the thallus, since those portions would have entered the soil which is the apparent source of infection. Such was found to be so when entire rhizoids were removed with a pair of forceps, stained with cotton blue and examined under the microscope. The passage of the hyphae was interrupted by the peg-like growths on the inner surfaces of the rhizoids and continuous hyphae, such as were frequently seen in smooth rhizoids, were not found. Hyphae often exceeded three in number in a single smooth rhizoid. Hyphae were also found

in the amphigastria on the lower surface of the thallus. Numerous sections through gemmae cups and portions of the thallus bearing archegonia showed that hyphae did not extend to or penetrate these structures. Careful investigation of the gemmae showed that they were entirely free from infection.

Nature of the fungus in the gametophyte.

The fungus is clear in longitudinal sections of the thallus and staining with cotton blue shows up the structure. Hyphae are frequently branched, have granular contents, are septate at irregular intervals and vary in thickness, the average being

Fig. 3. Infected cells of thallus showing penetration of cell walls. × 480.

about 4·6 μ. Although transverse sections were excellent for observing the actual zonation of the fungus, they were unsatisfactory for further detail. In longitudinal section, the hyphae were seen to run more or less parallel with the upper and lower surfaces, passing from cell to cell and giving off branches to

neighbouring cells. There is no apparent disorganisation of the cell wall when the fungus passes from one cell to another, and Ridler (1923) suggests that the penetration is mechanical, and not by enzyme activity. Sometimes there is a constriction in the hypha as it passes into a cell; the portion immediately within the cell wall is narrow but broadens out and assumes its average width in its passage through the cell (Fig. 3). Other hyphae show no marked constriction where they penetrate the cell wall.

Starch was found in the assimilating tissue and those portions of the thallus immediately above and below the fungal zone. Infected cells contained neither chlorophyll nor starch, a fact which was observed by Golenkin (1902) when he was studying

Fig. 4. Portion of ventral surface of thallus showing entrance of hyphae. × 400. *v.s.* ventral surface of thallus; *r.* rhizoid.

the fungus present in different species of *Marchantia*. The absence of starch from infected cells affords evidence of the absorption of carbohydrate material by the fungus.

Actual entrace of hyphae into the tissues of the thallus was frequently observed and two hyphae entering from a single rhizoid are seen in Fig. 4. Hyphae are always intra-cellular. Some cells were seen to be filled with a structureless mass which took the stain deeply. Small bits of hyphae were sometimes present in these masses and hyphae were seen passing directly into such cells and leaving them. These structureless organs represent sporangioles and are seen in Fig. 5. Clusters of very delicate and finely branched hyphae were seen in some neigh-

bouring cells, branching in a markedly dichotomous manner, and, although the magnification available was insufficient to determine any haustorial character, each branch was terminated by a conidium-like body which stained very deeply. These clusters represent arbuscules (Fig. 6), although those figured by Ridler (1923) do not indicate definite terminal structures to the fine hyphal branches. It has been held that these organs, arbuscules and sporangioles, represent two stages in the develop-

Fig. 5. Cells with sporangioles. × 480.

ment of the same structure, and Ridler suggests that the growth of the fungus is restricted by their formation and so prevented from becoming harmfully parasitic. The function of sporangioles is not, therefore, one of reproduction as the term might suggest. Vesicles (Fig. 7) were frequently observed. These structures were always terminal and showed marked variation in size. Vesicles observed by Cavers in *Fegatella conica* were both terminal and intercalary. Those in *Lunularia* have not been observed in an intercalary position. These organs contain

quantities of reserve food material and a somewhat general opinion is that in addition to their serving for immediate growth, they may ultimately function as reproductive organs after the death of the plant. If such is so in this liverwort, these vesicles are the only indications of any organs of reproduction of the fungus in the thallus. Pycnidia, which were produced in abundance when the fungus was isolated and grown on different agars, have not been observed in the tissues of the gametophyte.

Fig. 6. Cells with arbuscules. × 380.

Fig. 7. Portion of ventral surface of thallus showing hypha and vesicle in rhizoid. × 480.

Gallaud (1905) showed that endophytic mycorrhiza was common in Monocotyledons and Dicotyledons but, when growing as endophytes, spores are not formed and the systematic position of the fungi therefore remains doubtful. Although Gallaud's researches dealt with higher plants the same difficulty in identifying the fungus so repeatedly isolated from *Lunularia*, as the true endophyte, arises here where no fructifications of the fungus occur in the actual plant.

Isolation of the fungus.

Two media were employed, a glucose agar and a protein agar. These were composed as follows:

1. Glucose agar: 15 gm. agar, 15 gm. glucose, 1000 c.c. water.
2. Protein agar: 15 gm. agar, 10 gm. factory starch ± 0·63 per cent. protein, 5 gm. gluten, 5 drops hydrochloric acid, 1000 c.c. water.

The media were prepared in large flasks, sterilised in an autoclave and plates poured as desired.

Thalli were sectioned and examined under the microscope. Those heavily infected were selected as the most favourable from which to obtain the fungus. In such sections the fungal zone was outstanding and could be seen with the naked eye. Apparatus was carefully sterilised and every precaution taken to prevent contamination. All operations were carried out on blotting-paper which had been dipped in a 1 per cent. solution of mercuric chloride. Sections containing the fungus were torn with sterilised needles and the infected portions of the thallus placed on agar plates. Sub-cultures were made by removing fructifications under sterile conditions and placing these on fresh plates. All cultures were kept at laboratory temperature and covered by a bell-jar as a further protection.

Summary of results and identification of the fungus.

After an interval of about three days hyphae were seen radiating from the region where the inoculation had taken place. Optical observations indicated delicate, colourless hyphae which had covered the entire dish by the twelfth or fourteenth day. On the tenth day minute black dots appeared in a more or less confined area round the piece of tissue on the plate. The dots increased in size and number, assuming a definite structure and becoming scattered over the whole surface of the culture. The formation of these pycnidia was always accompanied by a change in the colour of the medium which deepened from pink to a purplish red. After removing bits of the fungus for microscopic examination, the cultures became contaminated usually by *Penicillium* and bacterial colonies.

The fungus consists of branched, septate hyphae with granular contents and varying in width. Occasionally H-shaped connections were found in hyphae removed from cultures. Ridler figures something similar in a rhizoid of *Lunularia*. De Bary (1887) points out that these H-connections result from coalescence of similar hyphae and are purely vegetative. Cavers

(1903), when examining living material of many liverworts, found from two to six hyphae passing up some of the rhizoids and sometimes showing ladder-like fusions.

Immediately before fruiting bodies were formed, microscopic examination showed some hyphae very much massed together. Such masses are considerably darker than the surrounding hyphae and indicate an early stage in the formation of pycnidia. Further development is marked by the dark brown or black colour of the wall and the characteristic shape when mature. Most pycnidia were flask-shaped with a definite neck or beak (Fig. 8). Others were more elongated and the neck, therefore,

Fig. 8. Single flask-shaped pycnidium and hyphae from culture. × 200.

not so well defined. Their dimensions (an average for twelve pycnidia) are as follows:

1. Flask-shaped pycnidium: Length, 112·5–165 μ; width (bowl area), 75–112·5 μ; width of neck, 22·5 μ.
2. Elongated pycnidium: Length, 350 μ; width, 30–60 μ.

When these fructifications were mounted on a glass slide, gentle tapping of the coverslip caused numerous oval spores to be emitted through the beak but sometimes resulted in breaking the pycnidium wall. The spores averaged 5·4 μ in length and 1·6 μ in width.

Preparations of the fungus isolated were identified by Mr J. Ramsbottom as a species of *Phoma**.

* *Phoma lunulariicola*. Pycnidiis atro-brunneis, ampulliformibus, 112·5–165 μ × 75–112·5 μ interdum elongatis 350 μ × 30–60 μ, poro singulo pertusis; sporulis ovoideis, hyalinis, 5·4 μ × 1·6 μ.
Mycelium e thallo *Lunulariae cruciatae*. Fructificat in vitro.

Discussion.

This *Phoma* shows some interesting points of difference from the fungus which Ridler isolated from the sporophyte of *Pellia epiphylla* (L.) Corda, and also identified as a *Phoma*.

In all infected plants of *Lunularia*, the fungus was confined to a zone below the assimilating tissue and never penetrated or approached the region bearing the reproductive organs of the plant, which were always archegonia. The fungus in *Pellia* was often in close proximity to the reproductive organs and in some when antherozoids had escaped from a mature antheridium, the cavity was filled with hyphae. No direct connection was observed, however, between the hyphae in the thallus and in the antheridium. The fungus was also found in the sporophyte of *Pellia*, although it had escaped observation for some time. Examination showed that hyphae from the thallus penetrated the foot, prevented elongation of the seta and discoloured the capsule. It is, however, impossible to draw any comparison between infected sporophytes of the two liverworts, as this generation is at present unknown in *Lunularia cruciata* in South Africa. Fructifications of the fungus have been found in *Pellia* but are unknown in *Lunularia cruciata*. Attempts to isolate the fungus from the thallus of *Pellia* were always unsuccessful. Ridler grew uninfected plants of this liverwort by placing spores on filter paper saturated with nutrient solutions in Petri dishes. Re-inoculation of such plants with the *Phoma* isolated from the sporophyte gave no positive results. As suggested by Rayner (1927, p. 172), it seems unlikely that the mycelia, which were found to occur in the gametophyte and sporophyte of *Pellia*, are related to one another.

Pycnidia were not found in the thallus of *Lunularia* and although the hyphae grown in culture are doubtless identical with those in the plant, the absence of any fructification of the fungus in the liverwort forbids absolute certainty at present. Moreover, complete proof would necessitate successful re-inoculation of the fungus isolated into uninfected thalli of the liverwort. As microscopic examination only indicates the presence of the endophytic fungus and especially since very few thalli have been found to be quite free from infection, no satisfactory result could be obtained by a chance re-inoculation. As gemmae were found to be quite free from infection, the possible solution seemed to lie in re-inoculating thalli produced in culture from such gemmae.

Although Ridler was successful in obtaining plants in this manner from gemmae of *Lunularia*, I have failed after repeated attempts. Ridler mentions that she isolated a pycnidium-

producing fungus from *Lunularia* but figures no fructifications and gives no measurements, so that I am unable to state that this is the same fungus. Ridler's attempts to re-inoculate the fungus she obtained into uninfected plants were not successful.

Infected and uninfected plants of *Lunularia* were always identical in appearance, both green, apparently healthy and with no difference in size. Cavers suggests that the presence of a fungus in *Fegatella* is correlated with the habitat and states that hyphae are always found when the substratum consists of rich humus, even when they are absent from plants of the same species growing on ordinary soils and stones. Although the clay loam on which *Lunularia cruciata* grows in the spruit at Johannesburg has no appreciable amount of humus content, it has been shown that the amount of fungal mycelium in the thallus is determined by the nature of the substratum. Ridler (1922) believed that the irregular distribution of infection in *Pellia* varied with the age of the thallus rather than with the habitat.

Where the endophyte was present in *Lunularia* no disorganisation of the tissues was observed, even in heavily infected plants. There was no discoloration nor any indication of disease as in *Pellia*.

It seems unlikely that this is an example of true symbiosis as uninfected plants are not inferior to those which contain the fungus. The fact that starch was absent from infected cells indicates that the fungus benefits but has no detrimental effect on the plant. Ridler's view that the association between the fungus and the liverwort is one of harmless parasitism on the part of the fungus seems the correct one. The constant occurrence of the endophyte in *Lunularia* and, moreover, the apparent harmony in which the two organisms exist would suggest a relationship brought about by prolonged adaptation.

This research was conducted in the Botanical Department of the University of the Witwatersrand, Johannesburg. I wish to express special thanks to Professor C. E. Moss for suggesting the research and for his willing help and advice. I should also like to thank Miss E. M. Young, M.Sc., for valuable suggestions in the part of the investigation dealing with the fungus.

Summary.

1. Only female plants of *Lunularia cruciata* (L.) Dumortier are found in South Africa.

2. The soil on which the liverwort grows was found to be slightly alkaline.

3. The gametophyte contains a fungus which is confined to a definite zone below the assimilating tissue. It occurs also in

the rhizoids and amphigastria but does not penetrate the gemmae cups and archegonia.

4. The fungus consists of branched, septate hyphae with granular contents, giving rise to vesicles, arbuscules and sporangioles which conform with the general type of endophytic fungus found in a great variety of higher plants. No fructifications of the fungus have been found in the tissues.

5. The endophyte of *Lunularia* has been isolated and identified as a species of *Phoma*.

6. The amount of fungus present appears to be correlated with the habitat of the plant.

7. The association between the two organisms is not true symbiosis, but rather harmless parasitism on the part of the fungus.

8. All plants, infected or uninfected, are green and apparently healthy. There is no indication of disease in the liverwort.

9. The fungus presents some striking contrasts from that recorded in *Pellia epiphylla* (L.) Corda.

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HELOTIUM SCUTULA (PERS.) KARST.: ITS GROWTH, DEVELOPMENT AND RESPONSE TO EXTERNAL STIMULI.

WITH SOME OBSERVATIONS ON H. CYATHOIDEUM (BULL.) KARST.

By Jessica H. Grove, M.Sc.

(With nine Text-figures.)

A SURVEY of literature has shown that the work done on the effect of light on fungi falls into three groups:

(1) *Abnormal forms*, often much elongated and branched, may be produced in darkness or in red or yellow light. Such forms were recorded as early as 1821 by Fries, who described abnormally developed species found in caves. A good summary of the work done before 1902 is given by MacDougall (1903), and detailed observations on *Lentinus lepideus*, *Polyporus squamosus* and various species of *Coprinus* are described by Buller (1909).

(2) *Spore formation* may be partly or entirely checked by darkness or absence of blue or violet light. The early work on this subject is summarised by MacDougall. Later investigations include those of Bayliss Elliott (1908) on *Polystictus versicolor*, the production of hymenium and spores in which is entirely inhibited by absence of light. Buller found the formation of the pileus of *Lentinus lepideus*, *Polyporus squamosus*, *Coprinus niveus* and *C. nycthemerus* to be entirely dependent on the stimulus of light. *C. plicatilis* and *C. ephemerus* were found to be unable to develop beyond a rudimentary stage, while *C. comatus* and *C. lagopus* were independent of light conditions. Dependence on light for the formation of hymenium and spores was found also in *Panus stypticus* (Johnson, 1920) and *Pyronema confluens* (Robinson, 1926).

(3) *Heliotropism.* Many fungi show well-marked heliotropic curvature during some period of development, the young stalk of the sporophore being frequently the sensitive organ, *e.g. Pilobolus* sp. (Parr, 1918) and others, *Sclerotinia cinerea* (Winter, 1874), *Coprinus* spp. (Brefeld, Buller); but sensitiveness is also recorded of the necks of perithecia of *Sordaria* spp. (Woronin, Winter) and in the asci of some *Ascobolus* spp. (Boudier, 1869) and of *Aleuria repanda* (Bayliss Elliott, 1927).

The majority of sensitive species recorded are Basidiomycetes, while among the Ascomycetes I have found sensitiveness to

light recorded for only twelve species, including one lichen. The following investigation was therefore undertaken in order to find the effect of light on two species of *Helotium*, *H. scutula* and *H. cyathoideum*, attention being paid chiefly to heliotropic curvature.

Helotium scutula.

During the autumn of 1927 large quantities of this species were found on dead stems of *Helianthus* sp. in a neglected garden. Fruit bodies were always seen to occur most abundantly on the upper side of the stems; the fungus was never found on completely buried stems, but especially in late autumn was abundant on those half-covered with debris. The apothecia here were borne on somewhat elongated stalks, and turned towards the light.

Stages in growth.

The development of the fruit bodies is very similar to that described by Hiley (1919) for *Dasyscypha calycina*. Three stages have been observed:

(*a*) In culture minute white tufts of hyphae first appear amongst the abundant superficial mycelium. This soon develops a solid core, at first perpendicular to the substratum. Under

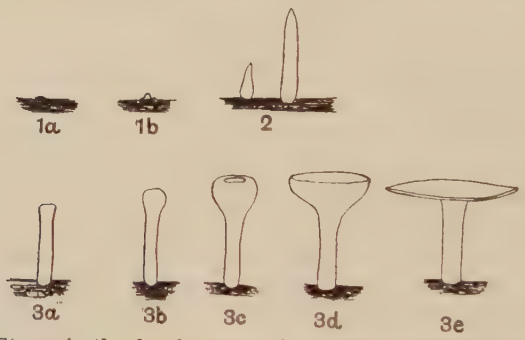

Fig. 1. Stages in the development of apothecia (diagrammatic.) × 8.

field conditions no superficial mycelium is formed, and the solid, pointed core is the first stage in the development.

(*b*) The white core soon begins to elongate, increasing in length for varying periods of time and to a greater or less extent under different conditions. This is the sensitive stage.

(*c*) Under suitable conditions the young, pointed stalk soon becomes blunted at the tip; the thickening increases until a globular head is formed, which gradually opens until the exposed hymenial surface is flat or slightly reflexed.

Heliotropic response.

1. Apothecia in different stages of development were kept in (*a*) darkness, (*b*) unilateral light, (*c*) daylight, for three weeks. Those in the stage of elongation continued to increase in length, turning upwards in darkness, or in light towards the source of strongest illumination. Fruit bodies in which disc formation had begun showed no change in direction.

2. Infected stems of *Helianthus* were scraped to remove all visible growth of the fungus, and replaced on the soil where they had been found. They were arranged in two groups—(*a*) in darkness, under an inverted plant-pot the hole of which was closed;

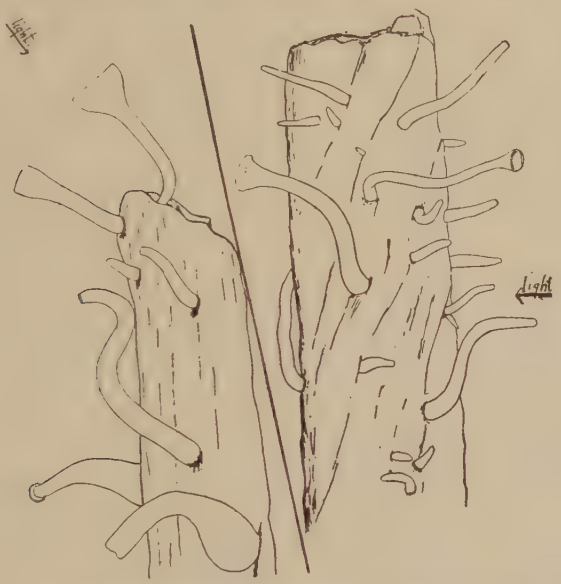

Fig. 2. Apothecia grown in tins, showing elongation and heliotropic curvature. × 5.

(*b*) covered with a similar pot admitting light from above through the hole. After twenty-six days numerous minute rudimentary fruit bodies had developed on the stems in darkness; even when left for a further fourteen days these progressed no further. During the same time, in addition to very numerous minute pointed bodies, five fully developed expanded apothecia had appeared in the pot to which light was admitted. When the pot was first removed, marked puffing of ascospores occurred, showing that the fruit bodies were mature. At the end of a further fourteen days they had shed their spores and decayed,

and other apothecia were developing. All the sporophores which developed under this plant-pot turned towards the light.

3. Scraped, infected stalks of *Helianthus* were placed on damp soil in four tin boxes, *A–D*. Light was admitted to *B*, *C* and *D* through narrow slits in the lid or side of the tins, *A* being in complete darkness. The boxes were kept in a window facing south-west and examined on the third day and afterwards at weekly intervals for ten weeks.

In the dark box, *A*, numerous apothecia reached the first conical stage, but developed no further.

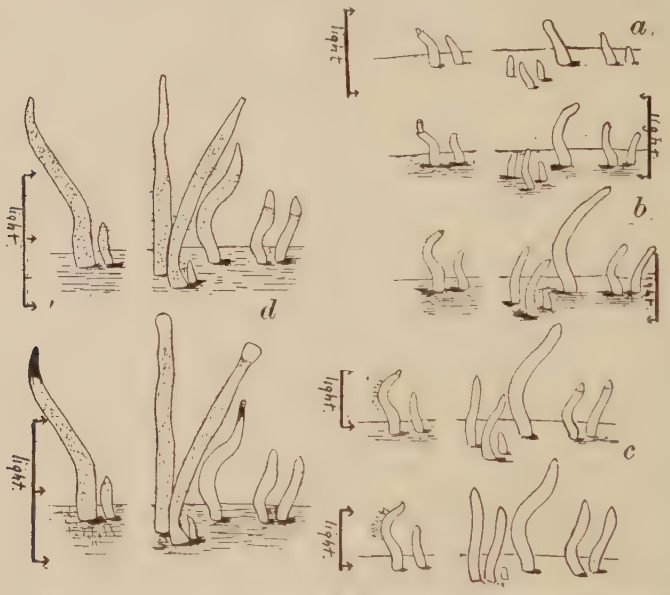

Fig. 3. Young sporophores grown on a klinostat in weak unilateral light, showing flocculence of stalks and heliotropic curvature. *a–d*, stages in growth. × 3.

In the lighted boxes, *B*, *C* and *D*, numerous apothecia in the initial stage were observed on the third day. By the eighth day they had reached a length of 2 mm., and many were turning towards the light. Growth continued, elongation and curvature being most marked near the slits, until at the end of the fourth week disc formation had begun. During the next few weeks numerous apothecia matured, and marked puffing was always seen on opening the boxes. The spores, though rather smaller than usual, proved capable of normal germination. The stalks of the apothecia varied in length from 10 to 15 mm., and when exposed to the dry air of the laboratory, in less than ten minutes

lost so much moisture as to become flaccid and incapable of supporting the disc.

Of the one hundred and forty-four apothecia counted, 64 per cent. were directed towards the light, and all but three of the remaining 36 per cent. turned towards the polished sides of the tins. Curvature was always much more pronounced near the slits, where direct light fell on the young fruit bodies, but reflected light from the polished surface of the tins appeared capable of inducing heliotropic curvatures.

4. Cultures bearing young pointed fruit bodies were kept in darkness in an upright position for a fortnight, a procedure known to increase their sensitiveness to light ((9) p. 463). The tube was then wrapped in a black paper case made to admit light from one end only, and attached in a horizontal position to a revolving klinostat to counteract the stimulus of gravity. The tube was examined and its position in the black case reversed at the end of one, two and three weeks. The first and second examinations showed marked curvature of the growing apothecial stalks towards the light, and considerable elongation. At the end of the third week, however, the first stage of disc formation was seen to have been reached, after which no further elongation or bending of the fruit bodies towards the light was observed.

5. The boxes used in (3) having been put aside for six months, a second crop of fruit bodies began to develop (July) which, when discovered, were without exception directed towards the slits in the boxes. No fruit bodies were formed in the dark box (*A*). These fruit bodies were found to be much more sensitive to light than those previously observed, a well-marked curvature following in less than twenty-four hours on a change in the direction of the light.

A series of experiments was made to find the effect of light of different wave-lengths on these pointed stalks, with the following results:

1. *Daylight.* Curvature in less than twenty-four hours, followed by elongation.

2. *Blue light.* No difference between this and daylight could be detected.

3. *Orange light.* No curvature produced; elongation continued at slower rate.

4. *Light through plain glass.* Curvature only visible a week later. Slow elongation.

The effect of daylight was tested again at the end of the series of experiments, to find whether the slow rate of response in (4) was due to the age of the fruit bodies. The response was not so rapid as in (1), but more marked than in (4), showing that full

daylight has a greater effect than weak light through glass, even on old sporophores, but that in light of the same intensity young fruit bodies are more sensitive than older ones.

During this series of experiments several of the pointed sporophores began to thicken at the tips and develop apothecia. No further heliotropic response was seen.

This series of experiments shows that the young pointed fruit bodies of this species are so sensitive to the directive influence of strong light that less than twenty-four hours' stimulation is needed to produce a marked curvature, and a spiral development of the young fruit body is produced by frequent change in the direction of the incident light. This recalls the observation of Woronin that the necks of the perithecia of *Sordaria fimiseda* are so sensitive to the directive influence of light that they develop in a zig-zag manner if their position with regard to the light be frequently changed.

Young sporophores are seen to be much more sensitive to light than those seven or eight weeks older, and when disc formation begins all heliotropic response is found to cease.

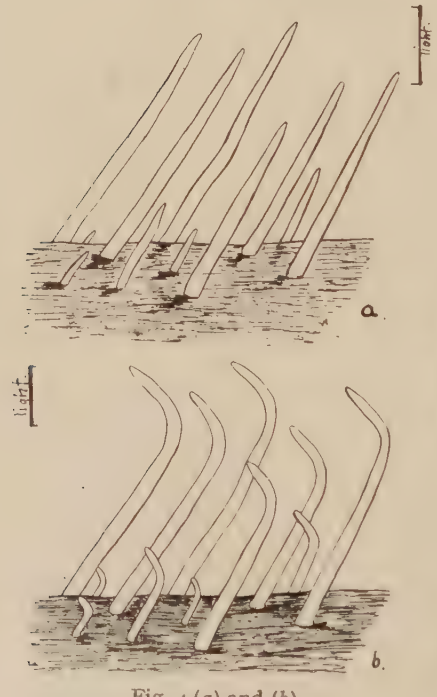

Fig. 4 (*a*) and (*b*).

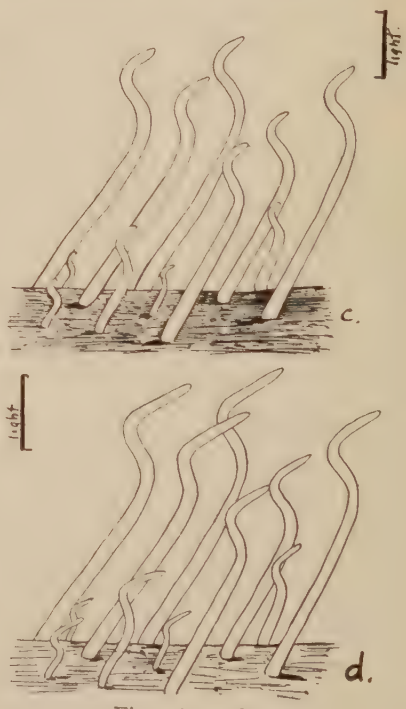

Fig. 4 (*c*) and (*d*).

Fig. 4 (*e*) and (*f*).

Fig. 4. Heliotropic curvature of young apothecia grown in tins. All × 4.
(*a*) The straight stalks as first observed.
(*b*) Curvature towards white light.
(*c*) Curvature towards blue light.
(*d*) Elongation in yellow light.
(*e*) Slight curvature to light through glass. *s.* sporophore which has not responded to light direction, disc formation having begun.
(*f*) Curvature towards white light.

Blue light is seen to exercise a heliotropic stimulus as strong as that given by daylight, but orange light produces no heliotropic response.

Geotropic response.

The conical pegs which are the first stage in the formation of apothecia arise perpendicular to their substratum. In darkness they fail to develop, but when exposed to light for a few days and then darkened again growth in length continues. No connection between the direction of light admitted and that of the subsequent growth in darkness could be observed. A culture containing elongating fruit bodies grown in the dark was again

placed in darkness in an upright position; in two days the sporophores had begun to turn upwards. The position of the tube was reversed, and after two days the young pointed fruit bodies were again turning upwards. This was repeated several times, until,

Fig. 5. Apothecia grown in darkness, showing negative geotropism. × 3.
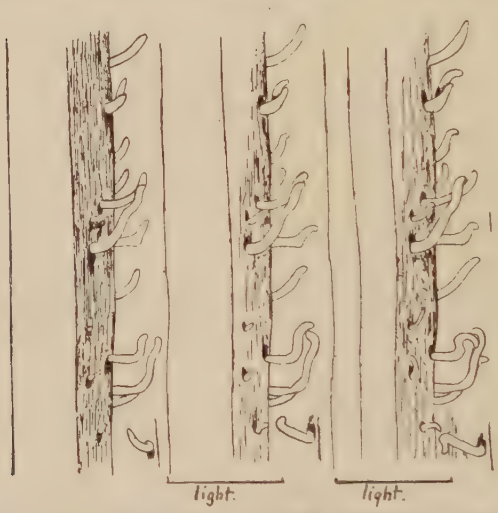
Fig. 6. Apothecia grown under the combined influence of light and gravity; growth in upward or downward direction. × 3.

after fourteen days, disc formation began, after which no further sensitiveness could be detected. This shows that the upward direction of growth in the young sporophores is a geotropic response.

When young elongating fruit bodies were exposed to light from below only, the directive influence of light was seen—especially near the source of light—to be stronger than that of gravity, for more than 50 per cent. of the young apothecia turned downwards.

Influence of light on development.

The young apothecia are found to be initiated in darkness, but in the absence of all light further growth in length does not occur. When elongation has once begun, however, further growth in length is found to be independent of light conditions.

Although apothecia were freely produced on infected stems placed in the open, the formation of mature apothecia has not so far been observed in tube cultures; the effect of light on their development has therefore not been investigated.

Response to light of *Helotium cyathoideum*.

At the end of October apothecia of this species were found growing abundantly on dead herbaceous stems, both on the surface and buried to a depth of about an inch in a garden rubbish heap, those buried being in almost complete darkness. When the heap was disturbed other stems thus brought to the surface developed mature apothecia in seven days, suggesting that they had been previously infected by the fungus mycelium even under conditions not suitable for the formation of apothecia.

Experiments on the growth of apothecia similar to those on *Helotium scutula* were made in tin boxes *A* (admitting light) and *B* (in darkness). In *A* (light) growth began after two days, and fully expanded apothecia with mature asci and spores were produced at the end of three weeks. Two weeks later all the spores had been shed and the fruit bodies had decayed.

In *B* (dark) growth was first observed ten days after the beginning of the experiment. Numerous apothecia, containing ripe asci and spores, were developed, which were slightly more elongated than those produced in the light. They did not fully expand, but remained wineglass-shaped, and the margins became wavy and deeply lobed. The shedding of spores and subsequent decay of the fruit bodies was not complete until three weeks later than in *A* (light). Thus in *Helotium cyathoideum* the production and liberation of the spores is retarded, though not completely inhibited by absence of light.

Since both in light and darkness the apothecia developed on all parts of the infected stems except those in contact with the box, and since no curvature of any kind could be detected, it was concluded that light and gravity have no effect on the direction of growth of the apothecia in this species.

Growth and development.

Collection of spores. The well-marked puffing of ascospores frequently observed on opening boxes containing ripe apothecia of *Helotium scutula* showed that the spores are forcibly ejected from the asci. Spores were therefore collected on a sterile coverslip placed in a ring culture chamber containing ripe apothecia kept moist with distilled water. The spores were shot up on to the coverslip in groups of from four to eight, according to the depth of the culture ring employed. All the spores appear to be shot as far as 5 mm. from the hymenial surface, and some to a distance of 10 mm.

Germination. Germination takes place in water in less than twenty-four hours, soon after the spore has become 1-septate; 1–3 germ tubes are formed, two being usual. Spores gathered at the beginning of the season (October) germinate much more rapidly than those gathered some months later.

Mycelium. A thin-walled, hyaline, septate mycelium rapidly develops, becoming densely matted by frequently anastomosing hyphae and by H-connections. Clamp connections have not been observed.

The completion of an H-connection was once observed. Two neighbouring hyphae were seen to bear short branches almost exactly opposite one another, at right angles to the main hyphae. The two branches grew straight onwards until only 2–3 μ apart, when the longer of the two was seen to bend its tip slightly towards the other, so that the two ends met. A pause ensued; then the tips of the hyphae appeared to melt into one another, at first in the centre only, but soon across their whole width, until no place of union was visible. The slight curve made when the one branch bent to meet the other could still be distinguished. The growth of the branches together across a gap of 4–6 μ, and their subsequent fusion, occupied about fifteen minutes. The temperature was that of the laboratory, about 12–14° C.

In all cultures more than a week old, spiral coils are found exactly resembling the "pelotons" described by Bernard (1909) as occurring in mycorrhizal species of *Rhizoctonia*. Their occurrence suggests that *Helotium scutula* may be a mycorrhizal species. Examination of the roots of the *Helianthus* with which it was found associated has so far failed to reveal any trace of mycorrhiza, though endophytic fungi not showing the characteristics of mycorrhiza have been observed in isolated cells of the root hair region.

Cultures. In addition to hanging-drop cultures in tap water, cultures were made in test tubes on dead stems of *Helianthus*, both those which had been previously infected and uninfected

stems being used. Dead stems of Michaelmas daisy and dead oak twigs were also employed. The stems were sterilised in steam in the test tubes, and infected with spores as long as these were available, and later in the season with mycelium from older cultures.

Whatever the substratum or method of infection, minute tufts of white mycelium became visible to the naked eye about a week after infection. The hyphae grew readily on the surface and also inside the stems in all cultures. Growth on wood and

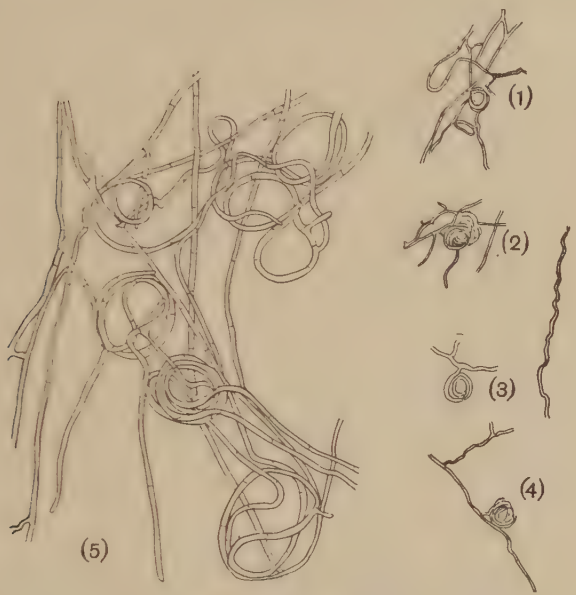

Fig. 7. Mycelium of *Helotium scutula* showing "pelotons." 1–4 × 120. 5 × 200.

on previously uninfected stems was more rapid than on stems which had previously supported fungal growth.

The hyphae continued to grow slowly for about two months, sometimes longer. On several occasions cultures were allowed to become dry, when all growth ceased, but fresh hyphae were produced as soon as water was added.

Fruit bodies. After about two months minute tufts of white hyphae began to appear in the cultures, gradually increasing in size. After from two to six weeks solid cores were formed, which in the light began to elongate to form pointed stalks resembling those known to be the first stage in the formation of fruit bodies. These were kept under varying conditions and used in some of

the experiments on response to stimuli already described. In some cultures the stems began to thicken at the tips, and in one, three half-expanded apothecia were produced, but fully developed apothecia with mature asci and spores were never produced in the culture tubes. Abnormal forms, sometimes much branched, were frequent, and once renewed growth occurred from the surface of a half-formed disc.

When the cultures were removed from their tubes and placed on damp soil in a garden, however, mature apothecia containing ripe asci and spores were produced in fourteen days. Several cultures which had been allowed to remain dry for two months began to show rudimentary fruit bodies the day after they were placed in the damp garden. The rapid revival of the mycelium which had lain dormant during two months' desiccation recalls the observations of Bayliss Elliott on the revival of desiccated mycelium of *Polystictus versicolor*, which, after being kept dry

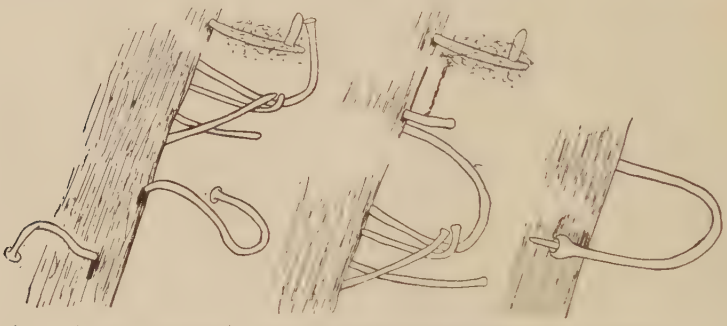

Fig. 8. Young apothecia; most advanced stage reached in culture. × 5.

for four years as a museum specimen, when placed in a damp chamber revived, and in a few weeks produced fruit bodies. That desiccated mycelium of *Coprinus sterquilinus* has been found to retain its activity for a year, as observed by Falck, and that the mycelium of *Psalliota campestris* retains its activity for considerable periods in compressed horse-dung bricks are further instances, quoted by Buller, of the power of mycelium to revive after desiccation.

Development under water. In contrast with the power shown by the mycelium of *Helotium scutula* of withstanding desiccation is the following observation of its growth under water. Stems of *Helianthus* which had been scraped free of all visible growth of apothecia were left standing in water, and were seen to develop young fruit bodies as far as the stage of elongation. These were abnormal in their growth, however, producing very irregularly curved stalks, the tips of which were often dichotomously

forked. Disc formation was not observed, though growth continued for some time. When, however, some of the young apothecia were exposed to the air owing to evaporation of the water in the jar, they developed half-expanded discs, but formed no ripe asci or spores.

Several months later it was observed that some of the young apothecial stalks which arose from time to time on these same sticks appeared to be thickening at the tips, the first visible stage in disc formation. They were very hairy, and when examined were found to consist entirely of hyphal tips, some densely filled with oily contents which turned black with iodine, and all appearing in an actively growing state. There was no sign, however, of a definite hymenial layer.

Distinction of the species.

A very close resemblance exists between *Helotium scutula* (Pers.) Karst. and *H. virgultorum* (Vahl) Karst. which lives on wood. The only differences apparent (according to Massee (11) and Rehm) appear to be the flocculent stem of the latter, the somewhat longer stem and smaller size of its asci and spores (*H. scutula* spores, 18–25 × 4–5 μ; *H. virgultorum* spores, 15–20 × 4–5 μ) and its difference of habitat. As *H. scutula* develops a flocculent stem in culture, frequently forms an abnormally long stem and spores rather smaller than the dimensions given, and can easily be made to grow on wood, and as it is moreover known to be a very variable species, it would seem that *H. virgultorum* is a variety of *H. scutula*, and not a distinct species.

Microscopic features.

Growth inside the stem.

Infected stems of *Helianthus* were fixed in chromacetic acid and serial sections about 10 μ thick were stained with Delafield's haematoxylin and eosin. Sections were made at different stages in the growth of the cultures:

(*a*) When tufts of white hyphae were first observed.
(*b*) On the first appearance of solid cores.
(*c*) At the beginning of the stage of elongation.
(*d*) When the apothecial discs were expanding.
(*e*) When ripe apothecia were present.

Transverse section showed abundant mycelium in all parts of the stem except the pith. Groups of infected cells were seen, the central parts of which were densely packed with coiled mycelium, resembling the "pelotons" which occurred in cultures. The outer cells of each group were less heavily infected, some containing only a single hypha. Single radial rows of infected

cells were also seen. When the hyphae passed from cell to cell they were very much constricted, connection being maintained by one or more thin threads.

Longitudinal section. Though some hyphae were seen passing transversely from cell to cell, the majority were observed to lie in a direction parallel to the axis of the stem. The hyphae were specially abundant in the xylem vessels, and frequently made use of the pits in passing from one cell to another. By testing with aniline chloride, xylem vessels in which hyphae occurred were shown to be delignified to a greater or lesser extent.

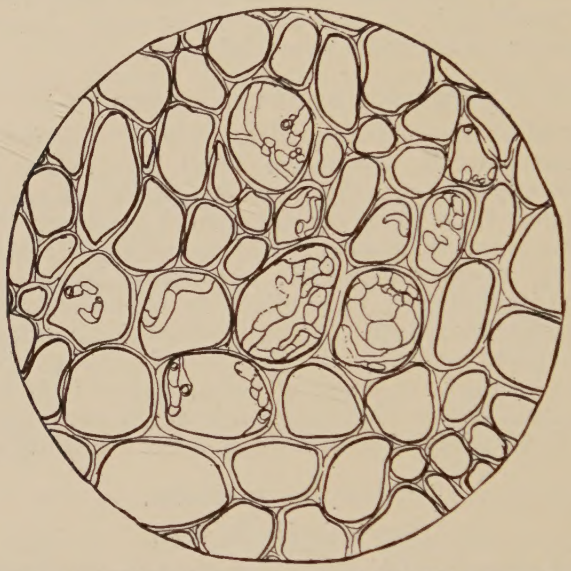

Fig. 9. Transverse section of stems showing intercellular mycelium. × 375.

Development of fruit bodies.

Numerous fruit bodies in different stages of growth were examined in the sections made. The stalks of the apothecia were seen to arise in the cortex of the infected stem, rupturing the epidermis by their growth. The cells near this point of attachment appeared full of deeply staining, granular contents, but no separate hyphae could be distinguished.

Search was made in the sections of various ages for some trace of sexual organs, but none was observed, either near the base of the stem or in the form of specially stainable hyphae in the stem or base of the cup. This search was an attempt to find a parallel in the Helotiaceae to the work of Duff (4) on members of the Geoglossaceae, by some considered an allied group. In three

of the four species investigated by him, Duff found a system of deeply staining generative hyphae, which proliferate with the tissues of the ascocarp and give rise to procarps or to ascogenous hyphae.

Conclusions.

1. Developing apothecia of *Helotium scutula* show marked positive heliotropism, the effect varying with the intensity of the light. The young fruit bodies behave in blue light as in daylight, in orange light as in darkness.

2. Young apothecia are negatively geotropic.

3. If exposed to the simultaneous influence of light and gravity, the former has the stronger influence on young apothecia.

4. The power of response to the influence of light and of gravity disappears as soon as the hymenial discs begin to form.

5. The fruit bodies are initiated in darkness but cannot develop without the influence of light. The early stages having been passed in light, development is able to continue in darkness.

6. In its response to the directive influence of light and gravity, and in its dependence on the stimulus of light for development *Helotium scutula* forms a marked contrast to *H. cyathoideum*. The latter develops normally in darkness, but spore production is retarded.

7. Fresh spores of *H. scutula* gathered at the beginning of the season germinate readily in water in less than twenty-four hours. Those gathered later in the season germinate much less readily.

8. The septate mycelium forms numerous, large, well-developed "pelotons" exactly resembling those of the mycorrhizal species of the genus *Rhizoctonia*.

9. The mycelium passes from cell to cell of the cortex and vascular tissue both transversely and longitudinally, making use of the pits of the wood vessels, and is constricted in its passage from cell to cell.

10. The sporophores originate below the epidermis of the substratum, breaking through when growth begins. Their development appears to be apogamous.

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